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Contents

Zoology Volume 39

Page

No 1 Towards a phyletic classification of the 'genus' *Haplochromis* (Pisces, Cichlidae) and related taxa. Part II; the species from Lakes Victoria, Nabugabo, Edward, George and Kivu
By P. H. Greenwood 1

No 2 A classification and the distribution of earthworms, suborder Lumbricina (Haplotaxida: Oligochaeta)
By R. W. Sims 103

No 3 Miscellanea
Notes on some Difflugiidae (Rhizopodea: Protozoa) from Norfolk
By C. G. Ogden 125
The genus *Azycocypridina* Sylvester-Bradley (Crustacea: Ostracoda) with particular reference to *A. imperialis* (Stebbing, 1901)
By J. Athersuch 139
Descriptions of two new and one poorly known species of the genus *Caligus* Müller 1785 (Copepoda: Siphonostomatoida)
By G. A. Boxshall and A. R. Gurney 161
A revision of the spider genus *Onomastus* (Araneae: Salticidae)
By F. R. Wanless 179
The genus *Atropacarus* Ewing (Acari: Cryptostigmata)
By B. W. Kamill and A. S. Baker 189
The first record of a rare murine rodent *Diomys* and further records of three shrew species from Nepal
By J. M. Ingles, P. N. Newton, M. R. W. Rands and C. G. R. Bowden 205

No 4 A revision of the spider genera *Asemonia* and *Pandisus*
By F. R. Wanless 213

No 5 Miscellanea
A revision of *Reophax* and its type-species, with remarks on several other recent hormosinid species (Protozoa: Foraminiferida) in the collections of the British Museum (Natural History)
By P. Brönnimann & J. E. Whittaker 259
The coelenterate taxa of Joshua Alder
By P. F. S. Cornelius & J. B. Garfath 273
A new genus of toad (Anura: Bufonidae) from the Republic of South Africa with remarks on its relationships
By A. G. C. Grandison 293
Aspects of breeding morphology in *Mertensophryne micranotis* (Anura: Bufonidae): secondary sexual characters, eggs and tadpole
By A. G. C. Grandison 299
A new species of *Crocidura* from Nigeria
By R. Hutterer & P. D. Jenkins 305

Bulletin of the British Museum (Natural History)

Towards a phyletic classification of the 'genus' *Haplochromis* (Pisces, Cichlidae) and related taxa. Part II; the species from Lakes Victoria, Nabugabo, Edward, George and Kivu

Peter Humphry Greenwood

Zoology series Vol 39 No 1 30 October 1980

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Contents

Introduction . . . 2
Methods and materials . . . 4
  Methods . . . 4
  Materials . . . 6
Classification . . . 6
  Astatotilapia Pellegrin . . . 6
  Harpagochromis gen. nov. . . . 10
  Prognathochromis gen. nov. . . . 14
    subgenus *Prognathochromis* nov. . . . 19
    subgenus *Tridontochromis* nov. . . . 20
  Yssichromis gen. nov. . . . 22
  Pyxichromis gen. nov. . . . 24
  Lipochromis Regan . . . 26
    subgenus *Lipochromis* Regan . . . 29
    subgenus *Cleptochromis* nov. . . . 31
  Gaurochromis gen. nov. . . . 32
    subgenus *Gaurochromis* nov. . . . 36
    subgenus *Mylacochromis* nov. . . . 36
  Labrochromis Regan . . . 37
  Enterochromis gen. nov. . . . 43
  Xystichromis gen. nov. . . . 46
  Neochromis Regan . . . 49
  Haplochromis Hilgendorf . . . 53
  Psammochromis gen. nov. . . . 53
  Allochromis gen. nov. . . . 57
  Ptyochromis gen. nov. . . . 60
  Paralabidochromis Greenwood . . . 67
  Hoplotilapia Hilgendorf . . . 72
  Platytaeniodus Boulenger . . . 75
  Macropleurodus Regan . . . 80
  Schubotzia Boulenger . . . 85
Lake Victoria haplochromines of uncertain generic relationship . . . 88
  'Haplochromis' cronus Greenwood . . . 88
  'Haplochromis' apogonoides Greenwood . . . 89
  'Haplochromis' theliodon Greenwood . . . 89
Lake Kivu haplochromines of uncertain generic relationship . . . 90
  'Haplochromis' schoutedeni Poll . . . 90
  'Haplochromis' wittei Poll . . . 90
Summary and conclusions . . . 91
Acknowledgements . . . 95
Guide to the identification of haplochromine genera in Lakes Victoria, Kioga, Nabugabo, Edward, George and Kivu . . . 96

Bull. Br. Mus. nat. Hist (Zool.) **39**(1): 1–101

Issued 30 October 1980

References 98
Index 100

Introduction

In the first part of this paper (Greenwood, 1979) I dealt at length with the philosophical and taxonomic problems posed by the polyspecific 'genus' *Haplochromis.* Applying a basically Hennigian approach to the problem (Hennig, 1966), I attempted to sort the fluviatile species of Africa and Israel into a number of monophyletic lineages. Since the interrelationships of these lineages could not be resolved cladistically, each was treated as having equal rank and classified as a genus (see Nelson, 1972).

The nominate genus, *Haplochromis,* was restricted to five species sharing a particular and highly derived form of dentition. All five are essentially lacustrine in habitat, and are confined to Lakes Victoria, Kioga, Edward, George, Nabugabo and Kivu (see Greenwood, 1979 : 278–281).

As in the first section of this review, the second part is concerned with an attempted arrangement of haplochromine taxa into presumed monophyletic lineages. Each lineage, as before, is recognized by its member species possessing uniquely derived features (synapomorphies). Where possible, the sister-groups of these lineages were determined but are not, at this stage of the revision, given any formal taxonomic status (save that of subgenus when that rank seemed the most appropriate one to indicate apparent relationship).

The taxa considered here are from the east African Lakes Victoria, Kioga, Edward, George, Nabugabo and Kivu. These lakes are well-known for the high levels of endemicity exhibited by their haplochromine species, and are interrelated through their hydrographical and geographical histories (see Greenwood, 1965, 1973 & 1974; and Fryer & Iles, 1972 for discussions and relevant literature).

A close taxonomic relationship between the '*Haplochromis*' species of these lakes, despite the high level of intralake endemicity, has long been acknowledged. But, this factor was, perhaps, overshadowed by the size and ecological complexity of the so-called *Haplochromis* 'species-flocks' in Lakes Victoria and Edward-George. Either explicitly, or implicitly, the flocks were assumed to be of mono- or at most oligophyletic origin (see Greenwood, 1974 : 19–20). In Lake Victoria it was thought that '. . . The existing species are certainly more closely related to one another than to any species outside the lake, and it seems justifiable to refer to the assemblage as a species flock' (Greenwood, 1974).

Research embodied in this paper readily falsifies that statement. Many lineages described below (*ie* groups of taxa sharing a recent common ancestry and therefore more closely related to one another than to members of another lineage) are composed of species from at least four of the lakes. Furthermore, it is rarely possible to establish, within a lineage, that the species from one lake are in fact each other's closest relatives. There are, of course, a few lineages known only from one lake (eg *Macropleurodus* and *Hoplotilapia* in Lake Victoria, and *Schubotzia* in Lake Edward–George), but the overall picture is one of a super-flock comprised of several lineages whose members cut across the boundaries imposed by the present-day lake shores.

Is it correct then, to continue using the term 'species flock' (= species swarm of Mayr, 1963) if the component species cannot be shown to stem from a single and fairly recent ancestor? Strictly the answer is 'no'; in future the term should be used sparingly and informally (whether to describe the haplochromines of one lake or of the lakes combined) and it should be employed more in an ecological than a taxonomic context.

Regrettably, no new data have emerged which might establish a monophyletic origin for the haplochromine species of Victoria–Edward–Kivu[1] (see also Greenwood, 1979 : 269). In other words, no uniquely derived character (or characters) has been found amongst all or the majority of haplochromines in these lakes.

---

[1] Since Lake Kioga is an extension of Lake Victoria, albeit one now isolated by the Owen Falls Dam at Jinja, Lake Nabugabo a cut-off bay of Lake Victoria (Greenwood, 1965 & 1974), and because Lakes Edward and George are in direct contact with one another (see Greenwood, 1973), the entire system can be referred to by the shorthand name Victoria–Edward–Kivu.

Anatomically, and particularly in their squamation patterns, the Victoria–Edward–Kivu species are of a basically *Astatotilapia* type, as they are in the occurrence of true ocelli on the anal fin of adult male fishes (see Greenwood, 1979 : 274–5 & 281–3). They far exceed *Astatotilapia,* however, in their range of body form, dental morphology, gill-raker shapes and number, and syncranial architecture (see Greenwood, 1973 & 1974). They also differ from fluviatile *Astatotilapia* in having a higher modal range of lateral line pore scales (31–33 **cf.** 28–30), the range extending to 36 (**cf.** 30, rarely 33 in riverine *Astatotilapia*), and in having a higher modal number of caudal vertebrae (16 **cf.** 15) and thus a higher count for the total number of vertebrae.

The ranges for both these counts, it should be noted, do overlap, although the lower values seen in fluviatile *Astatotilapia* species are rarely encountered in the Victoria–Edward–Kivu lineages (including species referred to *Astatotilapia* itself; see p. 8).

The significance of these differences is difficult to assess. A shift in modal values and in the end points of a range could, for such meristic characters, be genetically determined or might be the result of environmental factors acting during ontogeny. For the moment there are insufficient data on which to develop either argument further. This is, however, a problem that could have bearings on the possible monophyletic origin of the lake's super-flock (see above).

An earlier attempt to resolve phyletic relationships within the Lake Victoria *Haplochromis* flock (Greenwood, 1974) is now seen to be quite inadequate, and in many respects misleading when taxa from the historically related lakes Edward and Kivu are taken into account. The new arrangement, apart from suggesting a different grouping for certain taxa, also indicates that fewer species and lineages can be interrelated on a sister-group basis.

Outside lakes Victoria–Edward–Kivu, too, no sister-group relationships can be established for the lineages from those lakes. This situation may, however, change when the Lake Malawi haplochromines are studied more critically and within a cladistic framework.

At present, the former genus *Haplochromis* can be resolved into a number of apparently monophyletic lineages; the search for characters uniting these lineages through various levels of common ancestry must continue. More discriminating anatomical studies may reveal linkages so far undiscovered, and there would seem to be great scope for developing biochemical techniques directed towards that end.

In some respects it might seem that the application of a cladistic approach to the *Haplochromis* problem has failed, particularly when it appears impossible to construct dichotomously branching phylogenies at either the inter- or the intralineage levels (**cf.** for example, Vari's (1978) work on the teraponids which did achieve these goals).

It must be accepted that within any such polyspecific assemblage as the former taxon *Haplochromis,* some species will, through descent from a shared common ancestor, be more closely related to one another than to other species or groups of species. So far it has been possible only to make a first step towards discovering these relationships.

Yet, I believe that even this step could not have been made without the application of a basically Hennigian philosophy to the problem. In that way any morphological gaps (*ie* apomorph characters) have been used as positive characters to construct testable hypotheses (*ie* lineages) rather than as a means of ranking lineages through the subjectively estimated 'size' of the gap.

The creation of over twenty-five 'genera' where there was previously only one, has, I know, upset some of my colleagues who look upon my actions as those of a splitter run wild. But that indeed may have been the way in which the haplochromines (particularly the lacustrine species) evolved. To lump these lineages in a single genus (even as subgenera), whose monophyletic origin has not been established (and whose artificial and polyphyletic nature is strongly hinted at), is to hide the phylogenetic element of a classification. Regrettably, the constraints imposed by the Linnaean system of classification oblige one to use the formal rank of genus for the different lineages if one is not to be forced into implying a relationship that may not exist.

Part of the difficulty encountered in classifying the Victoria–Edward–Kivu haplochromines at both the inter- and intragroup level may be a consequence of their recent and explosive speciation (see Greenwood, 1974). Take, for example, the large number of *Astatotilapia* species in these lakes (page 8 below). All are remarkably similar, differing only in male coloration and minor (at any rate to the taxonomist) morphometric features. Any one of these anatomically and ecologically unspecialized species could be the nearest living relative of the ancestor to a lineage recognized by its one or, at most, its few derived features. In other words, one is dealing with a situation where the first phenotypically manifest 'marker' apomorphies have evolved only recently. It is thus impossible to recognize the plesiomorph sister group (or species) since the characters it shares with the derived sister species are primitive ones (*ie* symplesiomorphies).

Methods and materials

Methods

Little more need be added to the points discussed in the 'methods' section in the first part of this paper (see Greenwood, 1979 : 269–276), except to define certain characters not employed in that paper. These are concerned either with describing neurocranial shape or with the morphology of the jaw skeleton.

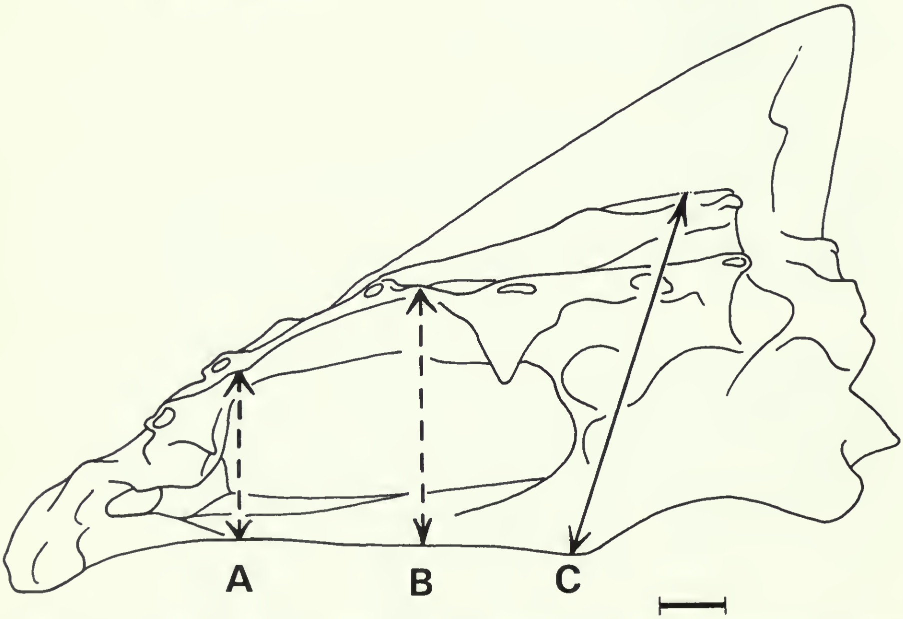

Fig. 1 Diagram to show reference points for various neurocranial measurements. A. Preorbital depth. B. Depth of orbit. C. Depth of otic region. (Solid line = direct measurement. Dashed line = to horizontal from parasphenoid margin.) Neurocranial outline from a skull of *Prognathochromis argenteus*. Scale = 3 mm.

Neurocranial length. The length of the skull measured directly[1] from the anterior tip of the vomer to the posterior point on the rim of the basioccipital facet for articulation with the first vertebra.

---

[1] That is, with the tips of the dividers actually contacting the points concerned, and the measurement then made between these points.

Preorbital depth. The depth of the skull through the anterior part of the orbit; measured in the vertical from the highest point on the horizontal surface of the frontal (*ie* disregarding the frontal wing which rises to meet the anterior tip of the supraoccipital) immediately above the point where the posterior margin of the lateral ethmoid meets the frontal, to the level of a horizontal line extended from the ventral face of the parasphenoid (see Fig. 1).

Depth of the otic region. The greatest depth measured directly[1] from the highest point on the supraoccipital base (*ie* excluding the crest), downwards and somewhat forwards to the lowest point on the parasphenoid posterior to the orbit (usually situated below the lateral commissure); see Fig. 1. It was necessary to choose the latter reference point as the ventral one because of considerable intra- and interspecific variability in the depth of curvature between that part of the parasphenoid and the articular surface of the pharyngeal apophysis.

Greatest width across the otic region. The maximum width of the skull as measured directly[1] across the pterotics.

Preotic skull length. Measured directly[1] from the anterior point of the vomer to the junction between the prootic and the ascending wing of the parasphenoid (*ie* near the base of the lateral commissure).

Depth of orbit. Measured vertically from the highest point on the curve of the frontal margin forming the dorsal rim of the orbit (ignoring the lateral line tubule if that should coincide) to a horizontal extended from the ventral margin of the parasphenoid in that vertical (Fig. 1).

Height of premaxillary ascending processes. Measured directly[1] from the bony distal tip of the processes to a point on the anterior face of the dentigerous arm (*ie* the beak or peak) level with the upper margin of its horizontal posterior prolongation (Fig. 2).

Length of premaxillary dentigerous arm. Measured directly[1] from the premaxillary symphysis to the posterior point on the horizontal arm.

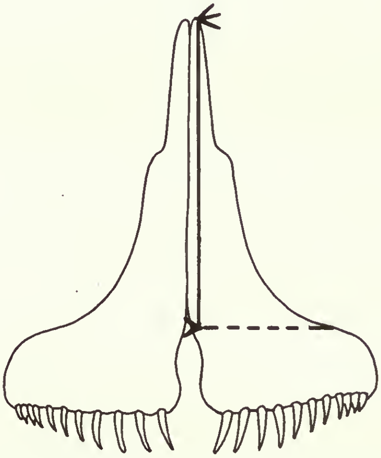

Fig. 2 Diagram showing reference points for measuring height of premaxillary ascending processes.

Length of lower jaw. Measured directly[1] from the symphysis to the posterior face of the anguloarticular bone immediately below the articular facet for the quadrate. All lower jaw measurements quoted were taken from whole specimens and, since some soft tissue is interposed between bone and divider point, these are fractionally greater than measurements taken from a skeleton.

The shape and proportions of jaw elements (dentary, anguloarticular bone, premaxilla and maxilla) in *Astatotilapia* species are taken to represent the plesiomorph (*ie* primitive) condition amongst haplochromines. This conclusion is based on the principle of commonality (see discussion in Greenwood, 1979 : 270). Departure from the *Astatotilapia* condition is, therefore, interpreted as being a derived (*ie* apomorph) state.

Such departures include bullation of the dentary in the region where it divides into ascending (coronoid) and horizontal arms; a change in various of its proportions so that the dentary no longer appears to be a slender, elongate bone but is relatively deeper and stronger, thereby assuming a stout, foreshortened appearance; and, finally, extensive lateral development of the dentigerous region so that its alveolar surface projects outwards as a distinct shelf overhanging the lateral wall of the dentary. Primitively, the symphysial region of the dentary is vertically aligned and narrow, and there is no distinct mental protuberance developed at its anteroventral angle.

Derived conditions in the anguloarticular are usually associated with a stout and foreshortened dentary; they include a general thickening of the bone, a reduction in its relative height (*ie* of the coronoid arm, the so-called primordial process of Barel *et al.*, 1976), and a change in the shape of its anteroventral projection (*ie* the arm which underlies the dentary), especially its anterior angle (which, primitively is produced and acute, but deepened and rounded or rectangular in its derived form).

Derived characteristics in the premaxilla include a lengthening of its ascending processes relative to the dentigerous arms, inflation of the dentigerous arms which thus become nearly cylindrical or distinctly ovoid in cross-section, and an increase in the width of their alveolar surfaces (a change generally but not invariably correlated with inflation of the arm itself). An expansion of the dentigerous arms anteriorly and anterolaterally, in the region below, and in front of the ascending processes, is also considered to be a derived condition. This gives the bone a 'beaked' or 'peaked' appearance.

The maxilla shows fewer changes in its morphology; chief amongst the derived conditions recognized are those in which the posterior part is relatively deepened, or is bullate, or when the articulatory head is turned medially at a marked angle (sometimes almost to form a right angle with the shaft of the bone). These apomorph conditions may occur together, in various combinations, or singly.

Materials

In addition to the specimens noted in Part I of this paper, all the BM(NH) haplochromine material from the five lakes has been involved in this review. It includes spirit specimens, dry skeletons (many prepared for this paper) alizarin transparencies, and radiographs.

Descriptions and comments are generally based on adult or subadult specimens. This is partly because the specific identity of juvenile and post-larval fishes cannot always be determined, and partly because some morphological features change during ontogeny (the dentition and some syncranial features are particularly liable to be affected in this way). However, where ontogenetic modifications appear to throw some light on problems of phylogeny, these have been taken into account.

Classification

In the generic diagnoses which follow, presumed apomorph (*ie* derived) features or conditions of a character-complex are italicized.

The serial listing of the genera should not be interpreted as having any particular phylogenetic significance. However, the most generalized taxon is taken first, and some of the more specialized lineages are dealt with later in the paper.

ASTATOTILAPIA Pellegrin, 1903

Several endemic species from Lakes Victoria, Kioga, Edward, George, Nabugabo and Kivu must now be added to this genus (see Greenwood, 1979 : 281 *et seq* for redescription and basic diagnosis of the genus). A typical *Astatotilapia* is shown in Fig. 3.

Unfortunately, this additional material in no way clarifies the status of the taxon, nor does it help to establish its monophyly. *Astatotilapia* remains, as before, a genus based on plesiomorph characters widely distributed amongst haplochromine cichlids; the one probable apomorphy (anal ocelli in male fishes) is shared by at least three other lineages (see Greenwood, 1979 : 268 & 284–5).

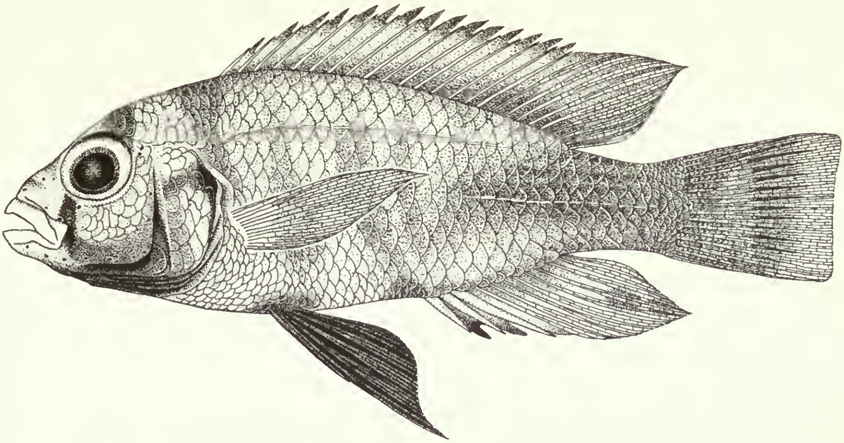

Fig. 3 *Astatotilapia elegans.* Lake George. About natural size.

The endemic *Astatotilapia* species from Victoria–Edward–Kivu differ from their fluviatile congeners in two major features: a higher modal number of lateral line pore scales (32–33 **cf.** 28–30) and a higher modal number of caudal vertebrae (16 **cf.** 15). In addition, not all the lacustrine species have several enlarged unicuspid teeth posteriorly in the outer premaxillary row (see Greenwood, 1979 : 282), although one or two such teeth are present in the majority.

There is an overlap in the total range of lateral line scale counts for fluviatile and lacustrine species (28–30, rarely 33, compared with 30–34 in the latter), but no lake species has a scale count in the lower part of the fluviatile range. Likewise, there is an overlap in the ranges for the number of caudal vertebrae, but again higher counts are confined to lake species (14–16 caudal vertebrae in fluviatile species, 15–17 in lake species).

Astatotilapia desfontainesi, from Tunisia and Algeria, is exceptional amongst the fluviatile taxa in having a high lateral line scale count (31–33), but its vertebral counts are typically those of fluviatile *Astatotilapia* species.

In most other respects the redescription of *Astatotilapia,* based on fluviatile taxa, given in Greenwood (1979 : 281–5) covers the species now included in the genus. Note may be made, however, that the range of gill raker numbers is increased to 13 (but the mode remains at 8 or 9), and that one of the newly included species (*A. oregosoma*) has a more slender body form than its congeners (30–34% SL **cf.** 35–40%).

The maximum adult size range is from 70 to 100 mm standard length.

Certain syncranial characters not discussed in Greenwood (1979) were found to be of value when dealing with the Victoria–Edward–Kivu haplochromines. These may be noted briefly, and are applicable both to the fluviatile and the lacustrine representatives of *Astatotilapia.*

Jaws. Over its posterior half, the lateral wall of each dentary is flared outwards. Consequently the alveolar surface is carried on a narrow, laterally produced shelf projecting slightly beyond the body of the ramus. The length of the entire lower jaw (dentary and anguloarticular) ranges from 31–46% of head length (modal range 40–43%).

The ascending processes of the premaxilla are shorter than the dentigerous arms, usually much shorter (about half the length) but in a few species only fractionally shorter. In all but one species (*A. velifer,* Lake Nabugabo) the dentigerous arms are compressed in cross section; *A. velifer* has the arms very slightly inflated and ovoid in section. No *Astatotilapia* species has the anterior and anterolateral aspects of the dentigerous arms drawn out into a beak- or shelf-like projection.

The maxilla is relatively short and deep, its articulatory head inclined medially at a distinct angle.

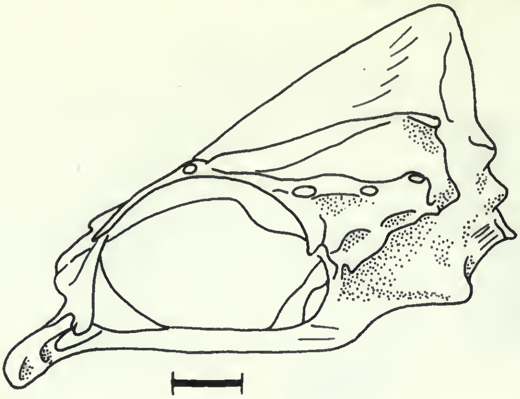

Fig. 4 Neurocranium (left lateral view) of *Astatotilapia macrops.* Scale = 3 mm.

Neurocranium (Fig. 4). Although the overall skull outline, especially the slope of the preorbital face, shows little intralineage variation, there is some variability in the profile of the supraoccipital crest. Most species have a relatively low crest with a distinctly wedge-shaped outline; in a few species, however, the crest is deeper and consequently its profile approaches the near-pyramidical shape found in members of certain other lineages (*A. bloyeti* typifies this condition in *Astatotilapia*; see Greenwood, 1979: fig. 6).

Preorbital skull depth in *Astatotilapia* ranges from 25–30% of neurocranial length, skull width from 50–61% (modal range 56–60%) and depth of the otic region from 43–50% (modal range 47–50%).

Contained species

Lakes Victoria, Kioga, Edward, George, Nabugabo and Kivu endemics only are listed; for the fluviatile species and those occurring in other lakes see Greenwood (1979 : 283–4).

Astatotilapia aeneocolor (Greenwood), 1973. Lake George; see Greenwood (1973 : 150–154).

Astatotilapia barbarae (Greenwood), 1967. Lake Victoria; see Greenwood (1967 : 93–97). Because of its partially paedophagous habits this species was previously associated with the major paedophage lineage *Lipochromis* (see p. 32 below and Greenwood, 1974). Anatomically, however, it shows none of the derived features characterizing *Lipochromis* (see Greenwood, 1967 : 96), and thus cannot be included in that lineage. Amongst *Astatotilapia, A. barbarae* is outstanding for its low otic skull depth (*ca* 43% of neurocranial length).

Astatotilapia brownae (Greenwood), 1962. Lake Victoria; see Greenwood (1962 : 142–9).

Astatotilapia cinerea (Blgr.), 1906. Lake Victoria; see Greenwood (1960 : 239–242).

Astatotilapia eduardi (Regan), 1921. Lake Edward; see Trewavas (1933 : 332). Poll (1932 : 42) considers *Haplochromis vicarius* Trewavas (1933) to be a synonym of this species.

Astatotilapia elegans (Trewavas), 1933. Lakes Edward and George; see Greenwood (1973 : 145–9), and Barel *et al.* (1976).

Astatotilapia engyostoma (Trewavas), 1933. Lake Edward; see Trewavas (1933 : 331–2). A poorly known species represented only by the holotype, a specimen now in very poor condition (see Greenwood, 1973 : 162).

Astatotilapia lacrimosa (Blgr.), 1906. Lake Victoria; see Greenwood (1960 : 230–233).

Astatotilapia latifasciata (Regan), 1929. Lake Kioga; see Regan (1929 : 390).

Astatotilapia macrops (Blgr.), 1911. Lake Victoria and possibly the Victoria Nile; see Greenwood (1960 : 236–9).

Astatotilapia macropsoides (Greenwood), 1973. Lakes Edward and George; see Greenwood (1973 : 162–7).

Astatotilapia martini (Blgr.), 1906. Lake Victoria; see Greenwood (1960 : 245–8). The sharply decurved head profile, and the golden-yellow body coloration in both sexes, make this an outstanding species amongst the *Astatotilapia* of Victoria–Edward–Kivu. Skull morphology is also atypical since the preorbital and orbital depths are above modal, and the preorbital skull profile is decurved and slopes steeply. Dentally and in other osteological features, however, it does not depart from the usual *Astatotilapia* condition. The relationship of *A. martini* can be reviewed when more is known about *'H' cronus* and *'H' apogonoides* (see pp. 88 & 89 respectively).

Astatotilapia megalops (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 4–7).

Astatotilapia melanopus (Regan), 1922. Lake Victoria; see Regan (1922 : 165–6). A taxon of uncertain status in the Lake Victoria flock.

Astatotilapia oregosoma (Greenwood), 1973. Lake George; see Greenwood (1973: 159–162). An unusual species amongst the *Astatotilapia* complex because of its shallow body (depth 30–34% SL, mean 32%) and elongate habitus.

Astatotilapia pallida (Blgr.), 1911. Lake Victoria and possibly the Victoria Nile; see Greenwood (1960 : 233–6).

Astatotilapia piceata (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 7–10).

Astatotilapia schubotziella (Greenwood), 1973. Lake George and probably Lake Edward; see Greenwood (1973 : 188–192). The previously suggested close relationship between this species and *Psammochromis schubotzi* (see p. 56 below, and Greenwood, 1973 : 192) was not corroborated by more detailed anatomical knowledge.

Astatotilapia velifer (Trewavas) 1933. Lake Nabugabo; see Greenwood (1965 : 319–324).

DISCUSSION

Nothing much can be added to the comments already made on this supposed lineage (Greenwood, 1979 : 269, remarks on the *A. bloyeti* species complex, and also pp 284–5). Even information derived from the additional taxa now referred to *Astatotilapia* has failed to isolate a single derived feature uniquely common to all, or even the majority, of *Astatotilapia* species.

Species endemic to the lakes do, however, differ from their fluviatile congeners in having higher modal numbers of lateral line scales and caudal vertebrae (see p. 7 above). Phylogenetically speaking, the significance of those features is difficult to assess. Members of all other lineages in the lakes have modes and ranges for these two features comparable with those of lake *Astatotilapia* (or, in some genera, even higher). But, there is, currently, no way of telling whether this should be identified as an ecophenotypic response, or the result of a distant shared common ancestry.

Taken in their entirety, the lacustrine *Astatotilapia* show a little more diversity in their syncranial and dental morphology than do the fluviatile species.

Amongst the species of Lakes Victoria, Edward and George there are some whose dental and pharyngeal jaw morphology, and, or, their feeding habits, vaguely foreshadow the definitive characteristics of certain other lineages. For example, the slightly enlarged lower pharyngeal bone (with its enlarged median teeth) in *A. pallida* suggests affinity with *Labrochromis* (see p. 37 below, and Greenwood, 1960 : 234); skull morphology, and a partially paedophagous diet in *A. barbarae* suggests *Lipochromis* affinities (see Greenwood, 1974); the unicuspid jaw teeth and partially piscivorous habits of large *A. brownae* hint at a relationship with *Harpagochromis* (see p. 10 below, and Greenwood, 1974); the slender body-form of *A. oregosoma* resembles that in *Yssichromis* (see p. 23 below), and

A. schubotziella has certain features that suggest it might be related to *Gaurochromis* (see p. 32 below, and Greenwood, 1973 : 192).

However, in none of these examples is the resemblance either sufficiently clear-cut, or reflected in unequivocally derived morphological features, for it to be used as a reliable indicator of phyletic relationship. Hence, all these taxa are included in *Astatotilapia* and not in the lineage with some or all of whose members they seem to bear some resemblance.

It has not proved possible to demonstrate intralineage relationships between the numerous *Astatotilapia* species because the synapomorphies that would permit such an analysis were not discovered.

HARPAGOCHROMIS gen. nov.

TYPE SPECIES: *Hemichromis serranus* Pfeffer, 1896 (Type specimens in the Humboldt Museum, Berlin); see Greenwood (1962 : 152–6).

ETYMOLOGY. The name is derived from the Greek *harpage*, meaning a robber + *chromis*, a word, when used in such a combination, is now associated with many genera of African Cichlidae; it refers to the predatory habits of species in this lineage.

DIAGNOSIS. Robust and deep to relatively deep-bodied haplochromines (body depth 30–42% of standard length, modal range 34–36%), *reaching a large maximum adult size (146–200 mm SL).* Mouth generally horizontal or slightly oblique, but sometimes distinctly oblique; *lower jaw long (43–61% of head length, modal range 47–54%)* and with a prominent mental protuberance. Anterior and anterolateral regions of the premaxilla not produced to form a distinct beak or peak.

Neurocranium essentially of the generalized type, *but with a shallower otic region (40–44% neurocranial length* cf. *47–50% in the generalized type)* and a higher supraoccipital crest which is generally near pyramidical in outline. Preorbital skull depth 23–28% neurocranial length, mean 25%, skull width 54–60% (no distinct mode), greatest orbital depth 25–31% (modal range 25–28%).

Outer jaw teeth strong and recurved, unequally bicuspid and a few unicuspids in fishes <90 mm SL, the proportion of unicuspids increasing in larger fishes until, in specimens >120 mm SL, only unicuspids are present; outer row in premaxilla with 48–80 teeth (modal range 60–70). One or 2 (less commonly 3, rarely up to 5) inner rows of teeth in each jaw.

Cheek fully scaled, generally with 4 or 5 rows of scales (less frequently with 2, 3 or 6 rows).

DESCRIPTION

Habitus (Fig. 5). Most members of this lineage have a deep or moderately deep body (30–42% SL) which is never manifestly compressed. Head shape, and particularly the angle of the mouth, show some intraspecific variation, the mouth angle varying from almost horizontal (*Harpagochromis victorianus, H. serranus, H. michaeli*) to distinctly oblique (*H. cavifrons, H. plagiostoma,* see Fig. 5B).

Anatomically, osteologically and in their dentition, *Harpagochromis* species depart but slightly from the generalized condition typified by species of *Astatotilapia.* All, however, reach a much greater maximum adult size (146–200 mm SL cf. 60–100 mm), and most only attain sexual maturity at a length which is never reached by an *Astatotilapia* (*ie* at a standard length of more than 100 mm in *Harpagochromis,* modally between 120 and 140 mm, compared with lengths of 50–80 mm in *Astatotilapia*). The adult size reached by species of *Harpagochromis* is, with few exceptions, also greater than that attained by members of most other lineages (but see p. 14 below).

In some morphometric features, especially in having a relatively longer lower jaw and, less noticeably, a relatively smaller eye and deeper cheek (two characters generally correlated), *Harpagochromis* species differ from *Astatotilapia,* at least in modal values. The lower jaw in *Harpagochromis* is 43–61% of head length (modal mean values 47–54%), eye diameter 17–29% (modal mean values 20–24%) and cheek depth 22–37% (modal mean values 27–32%). There is a slight overlap in the ranges of these ratios when large specimens of

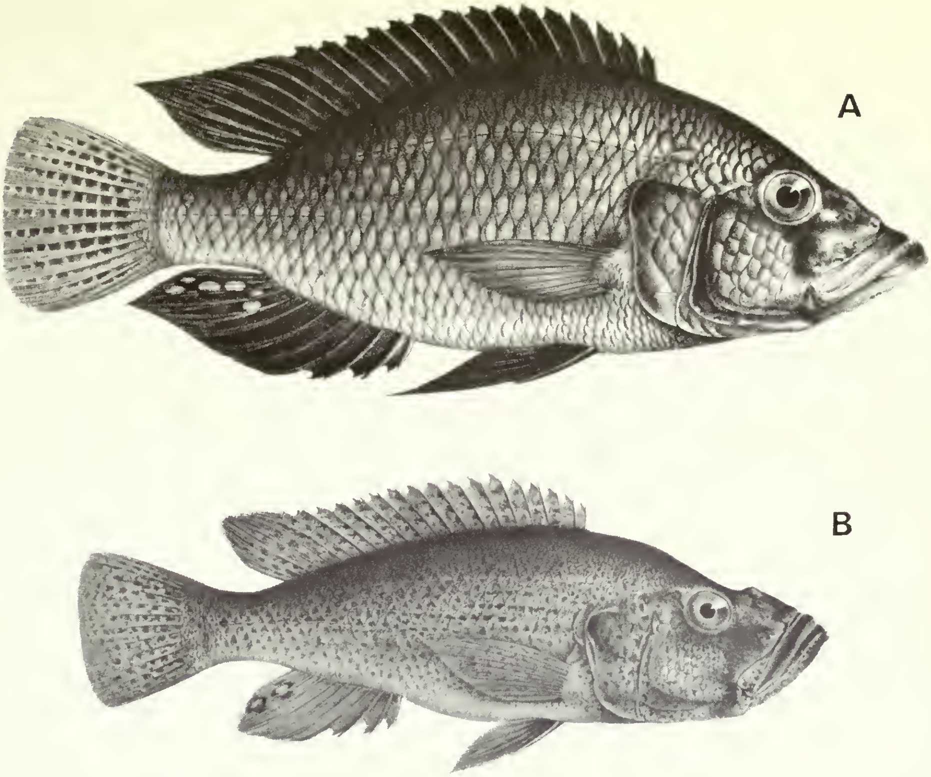

Fig. 5 A. *Harpagochromis spekii.* Lake Victoria. About half natural size. B. *Harpagochromis cavifrons.* Lake Victoria. About three-quarters natural size.

Astatotilapia species are compared with equal-sized *Harpagochromis* individuals. Since the characters in question invariably show either a positive or a negative allometry with body length, this overlap is to be expected. However, the modal value for lower jaw length is always higher for *Harpagochromis.* This might suggest that increased jaw size in *Harpagochromis* is not entirely attributable to allometric relationships with overall body size. In other words, it is in itself a derived feature, which is further emphasised through that allometric relationship.

Squamation. The cheek is fully scaled, usually with 4 or 5 rows of scales (less frequently 2, 3 or 6 rows); there are 30–34 (modal range 32–33) scales in the lateral line series.

Neurocranium (Fig. 6). The neurocranium in *Harpagochromis* is similar to that in *Astatotilapia,* except that the otic region is shallower (40–44% of neurocranial length **cf.** 47–50%) and the supraoccipital crest is higher and pyramidical in outline. Because the skull is deep preorbitally and orbitally, and since it is wide in the otic region, it is less obviously streamlined than is the skull form characterizing the other major piscivore lineage, *Prognathochromis* (see p. 16). Also, as compared with that lineage, the supraoccipital crest in *Harpagochromis* is taller relative to skull length, and slopes downward and forward more steeply.

Dentition. Fishes over 90 mm SL mostly have strong, somewhat recurved unicuspid teeth in the outer row of both jaws. Smaller specimens have predominantly bicuspid outer teeth, the cusps of unequal size, and the crown and upper neck slightly recurved. There are 48–80 outer teeth in the premaxillary series (modal range 60–70).

Inner row teeth are either tricuspid, unicuspid or a mixture of both types, arranged in 1 or 2 (less frequently 3) rows anteriorly and anterolaterally.

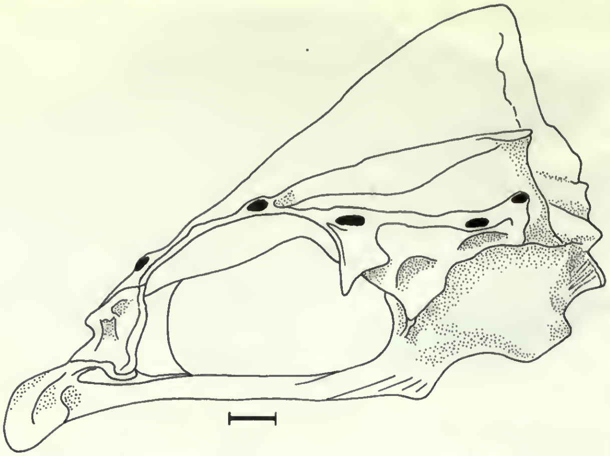

Fig. 6. Neurocranium (left lateral view) of *Harpagochromis maculipinna*; scale = 3 mm.

Jaws. The proportionally long lower jaw has been noted already. In all other respects it barely departs from the *Astatotilapia* type, apart from having a well-developed mental protuberance at the base of the symphysis. In some species the crown of the coronoid process (the ascending dentary limb) has a distinct lateral deflection.

The anterior and immediately lateral regions of the premaxilla are but slightly produced forward (Fig. 7), so that in lateral view it is hardly beaked (**cf.***Prognathochromis,* p. 18). The dentigerous arms are very slightly inflated, and have a compressed ovoid cross-section.

Vertebral numbers: 28–31 (mode 30), comprising 12–14 (mode 13) abdominal, and 15–18 (modes 16 or 17) caudal elements (the fused PU_1 and U_1 centra excluded).

Caudal fin. Most species have the posterior margin truncate or weakly subtruncate, but in one species (*H. plagiostoma*) it is obliquely truncate, that is, sloping forward and downward to meet the upwardly curved ventral region.

Contained species

The taxa are arranged in groups approximating to their degree of morphological departure from the generalized '*Astatotilapia*' bauplan.

Harpagochromis serranus (Pfeffer), 1896. Lake Victoria; see Greenwood (1962 : 152–5).
Harpagochromis victorianus (Pellegrin), 1904. Lake Victoria; see Greenwood (1962 : 156–8; plate I).

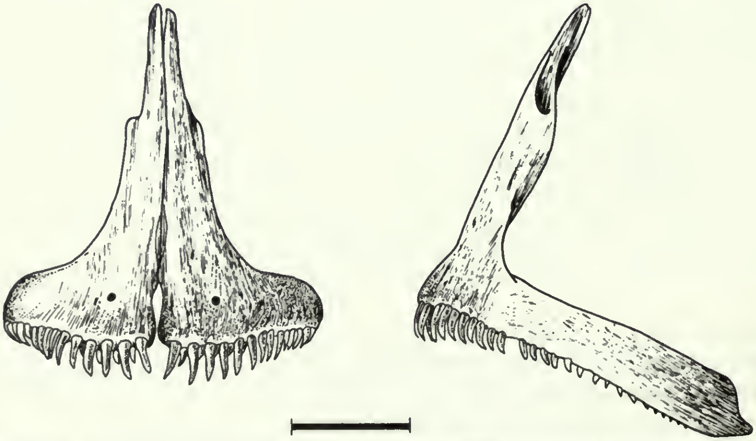

Fig. 7 Premaxilla of *Harpagochromis maculipinna*, seen anteriorly and in left lateral view. Scale = 5 mm.

Harpagochromis nyanzae (Greenwood), 1962. Lake Victoria; see Greenwood (1962 : 159–161).

Harpagochromis spekii (Blgr.), 1906. Lake Victoria and the Victoria Nile; see Greenwood (1967 : 32–38).

Harpagochromis maculipinna (Pellegrin), 1913. Lake Victoria; see Greenwood (1967 : 43–47).

Harpagochromis squamipinnis (Regan), 1921. Lake Edward and George; see Greenwood (1973 : 204–9).

This species differs from all its congeners in Lake Victoria (and all known haplochromine species) in having short rows of small scales extending from the body onto the membrane of the dorsal and anal fins. The scales are closely applied to the fin rays, both spinous and branched (see fig. 31 in Greenwood, 1973 : 206). In its gross morphology *H. squamipinnis* closely resembles *H. serranus* and *H. victorianus* of Lake Victoria. At present no other *Harpagochromis* species are known from Lakes Edward and George.

Harpagochromis boops (Greenwood), 1967. Lake Victoria; see Greenwood (1967 : 47–49).

Harpagochromis pachycephalus (Greenwood), 1967. Lake Victoria; see Greenwood (1967 : 39–42).

Harpagochromis thuragnathus (Greenwood), 1967. Lake Victoria; see Greenwood (1967 : 49–51).

Harpagochromis guiarti (Pellegrin), 1904. Lake Victoria; see Greenwood (1962 : 145–9). The distribution recorded in that paper included Lake Edward; this was based on earlier identifications of material from Lake Edward which most probably does not belong to this species (see Greenwood, 1973 : 232). The identity of the Edward material, and the true distribution of *H. guiarti,* must await the outcome of further research on the haplochromines of Lakes Edward and George.

Harpagochromis artaxerxes (Greenwood), 1962. Lake Victoria; see Greenwood (1962 : 170).

Harpagochromis altigenis (Regan), 1922. Lake Victoria, see Greenwood (1967 : 60–65).

Harpagochromis pectoralis (Blgr.), 1911. Lake Victoria. This species was given the replacement name '*squamulatus*' by Regan (1922), since at that time '*pectoralis*' would have been a junior homonym of *Haplochromis pectoralis* (Pfeffer), 1893. Because Pfeffer's species is now placed in the genus *Ctenochromis,* for which it is indeed the type species (Greenwood, 1979 : 287), the original trivial name for Boulenger's 1911 species can be resurrected.

Harpagochromis pectoralis differs from other members of the lineage in a number of features, but especially in having a more strongly decurved preorbital skull profile. Its relationships with (or within) the *Harpagochromis* lineage may have to be reconsidered when several undescribed and '*pectoralis*'-like species from Lake Victoria have been studied.

The species is redescribed in Greenwood (1967 : 60–65).

Harpagochromis plagiostoma (Regan), 1922. Lake Victoria; see Greenwood (1962 : 199–202).

Harpagochromis cavifrons (Hilgendorf), 1888. Lake Victoria and possibly the Victoria Nile; see Greenwood (1962 : 196–9).

Harpagochromis michaeli (Trewavas), 1928. Lake Victoria; see Greenwood (1962 : 203–6).

Incertae sedis

'Haplochromis' diplotaenia Regan & Trewavas, 1928, Lake Victoria. This species is known from very few specimens, and no skeletal material is available. Judging from radiographs its

neurocranial architecture is of the *Harpagochromis* type, but the difficulties associated with obtaining accurate measurements from radiographs preclude definite conclusions on that point.

'Haplochromis' paraplagiostoma Greenwood & Gee, 1969. Lake Victoria. Again, a shortage of osteological material has made it impossible to check several critical features. Although superficially this species does resemble other members of the *Harpagochromis* lineage, it seems advisable to keep the generic placement of *'H'. paraplagiostoma* as *incertae sedis* until more specimens are available for study.

'Haplochromis' worthingtoni Regan, 1929. Lake Kioga. Known only from the holotype (141·0 mm SL), this species closely resembles species of the *Harpagochromis serranus—maculipinna* group in all visible anatomical features. From a radiograph its neurocranium also seems to be of a *Harpagochromis* type.

DISCUSSION

The phyletic integrity of this presumed lineage depends on a single synapomorphy, the attainment of a large adult size (with which is, of course, associated a number of other characters, see p. 11 above).

There are indications that members of this lineage, as compared with species of the genus *Astatotilapia,* do have a basically longer lower jaw over and above the relative increase in jaw length effected through its positively allometric growth pattern.

Anatomically, most *Harpagochromis* species retain a generalized level of organization like that in *Astatotilapia.* Only two species, *H. plagiostoma* and *H. cavifrons,* with their very oblique mouths, show some departure from that condition, while a third (*H. pectoralis*) has a slightly derived type of skull architecture.

The possible relationship between *Harpagochromis* and *Prognathochromis* (as suggested in Greenwood, 1974) is discussed on p. 22.

Although the list of *Harpagochromis* species (p. 12) is arranged so that morphologically similar species are grouped together (in order of increasing departure from the *Astatotilapia* level of organization), this should not be taken to imply true phyletic relationships. Such intralineage relationships cannot be determined on the basis of data currently available.

PROGNATHOCHROMIS gen. nov.

TYPE SPECIES: *Paratilapia prognatha* Pellegrin, 1904; see Greenwood (1967 : 78).

ETYMOLOGY. The name is derived from that of the type species.

DIAGNOSIS. Body form variable, from shallow to deep (24–45% standard length) but most species relatively slender (body depth 30–34% SL) and none is markedly compressed. *Lower jaw long (41–62% head length, modal range 45–53%)* and with a prominent mental protuberance; premaxilla distinctly beaked or peaked.

Overall habitus one of a slender, streamlined fish with a large, often oblique mouth, and the head with a relatively acute entry angle. Maximum adult size extending over a wide range of lengths (70–230 mm SL), but most specimens reaching 140–200 mm SL.

Neurocranium (the principal diagnostic feature, particularly for differentiating *Prognathochromis* from *Harpagochromis*), *elongate, slender and shallow, with a low, supraoccipital crest,* wedge-shaped in lateral outline. *Preorbital skull depth 18·6–23·% of neurocranial length (mode 21%), greatest orbital depth 22–28% (modal range 22–23%), depth of otic region 31–42% (no distinct mode), skull width 42–55% (modal range 47–50%),* all expressed as ratios of neurocranial length.

Teeth in outer row of both jaws strong and recurved, mostly unicuspid in fishes >90 mm SL, unequally bicuspid with some unicuspids in smaller fishes. Thirty-four to 94 outer teeth in the premaxilla, modal range in the nominate subgenus 50–60, but 66–74 in the other subgenus. In that subgenus, whose members have a small adult size (95–120 mm SL), *tricuspid teeth occur laterally and anterolaterally, interspersed amongst the predominantly* *unicuspid outer teeth.* The inner teeth in both subgenera are uni- or tricuspid, and are arranged in 2 or 3 (rarely 1, 5 or 6) rows anteriorly and anterolaterally.

Cheek fully scaled, usually with 3 or 4 rows but sometimes 5 or 6, rarely with only 2.

Description

Habitus (Fig. 8). Body form is variable, the depth varying from shallow to relatively deep (24–45% SL) but moderately shallow in the majority of species (modal range 30–34% SL). Except in a few species, the body is not noticeably compressed.

With few exceptions, members of this genus have a 'typical' predator facies (see Fig. 8; and figs 13–15 in Greenwood, 1974), *ie* a slender streamlined body, large mouth and a predominantly unicuspid dentition. In all these features, *Prognathochromis* represents a marked development of the habitus-type beginning to appear in the *Harpagochromis* lineage. No

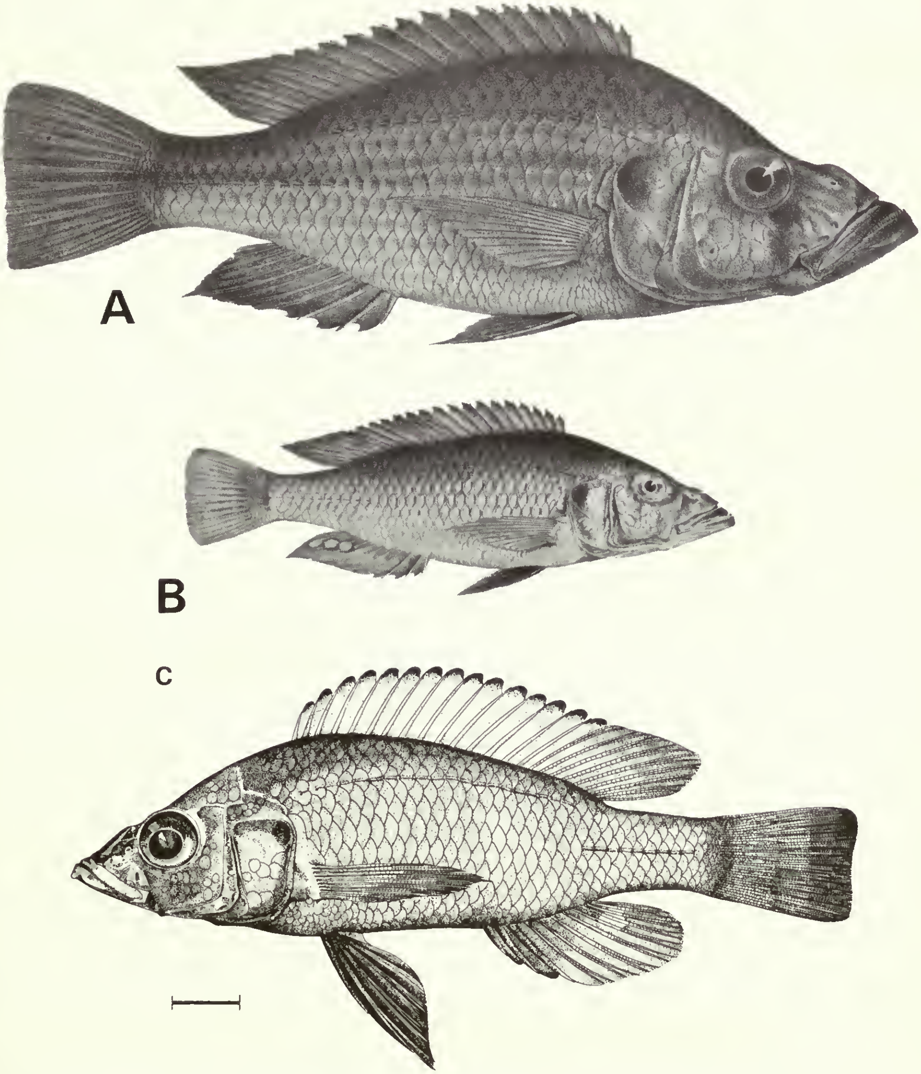

Fig. 8 A. *Prognathochromis (P.) prognathus.* Lake Victoria. About four-fifths natural size. B. *Prognathochromis (P.) mento.* Lake Victoria. About half natural size. C. *Prognathochromis (Tridontochromis) sulphureus.* Lake Victoria. Scale = 1 cm.

member of the *Prognathochromis* line retains the near-*Astatotilapia* habitus which characterizes so many species of *Harpagochromis.*

Nine species attain only a small adult size (70–120 mm SL), but for the others the maximum size lies in the range 140–230 mm SL.

As would be expected, those species reaching a small maximum size have, as compared with their larger congeners, relatively larger eyes and shallower cheeks (24–34% head length, modal range 27–30%, and 16–29%, modal range 19–22% head length, for the characters respectively). In these features they depart but slightly from the generalized condition. Species reaching greater maximum sizes (modally 150–200 mm SL) have relatively smaller eyes (17–26% head, modal range 19–22%) and somewhat deeper cheeks (18–33% head, modal range 24–26%).

The angle of the mouth varies from near horizontal to markedly oblique, and the lower jaw is long (41–62% head, modal range 45–53%). As in *Harpagochromis,* the relative lower jaw length is greatest in larger individuals, but even in those species with a small adult size (*ie* < 110 mm SL), the mean lower jaw length is distinctly greater than that in comparable sized *Astatotilapia* species. It is also greater than in most species of other, but non-piscivorous, groups.

Squamation. The cheek is fully covered by 3 or 4 (less commonly 2, 5 or 6) rows of scales, the lateral line has 30–34 scales (modes 32 or 33), rarely 35.

Neurocranium (Fig. 9). A slender, shallow and generally streamlined neurocranium is found in all species of *Prognathochromis* (see Fig. 9; and fig. 69 in Greenwood, 1974).

Preorbital skull depth is from 18·6–23·1% of neurocranial length (mode 21%), greatest orbital depth 21·7–28·0% (modal range 22–23%), and the greatest width across the otic region 42–55% (modal range 47–50%). Preotic skull length varies from 63–70% (mode 66%) of neurocranial length, and is thus virtually identical with that in *Harpagochromis.*

In most species the supraoccipital crest is low (particularly in relation to that in *Harpagochromis*), and it slopes gently downwards and forwards. The outline of the crest is thus more nearly wedge-shaped than is the pyramidical crest in *Harpagochromis* (and in a few *Prognathochromis* species, eg *P. xenostoma* and *P. flavipinnis*; however, even in these taxa the crest is relatively low and the rest of the skull has proportions typical for the lineage). A wedge-shaped crest characterizes the presumed generalized haplochromine skull (eg *Astatotilapia bloyeti,* see fig. 6 in Greenwood, 1979), but it is relatively lower in *Prognathochromis.*

Within *Prognathochromis* there is a graded range of skull forms (see Greenwood, 1962 : 208, fig. 25; 1967 : 108–115; and 1974 : 98, fig. 69) but even in those species with the least derived skull form (eg *P. melichrous, P. dichrourus, P. arcanus*), gross neurocranial morphology is quite distinct from that in other lineages.

There is also some variation in the form of the ethmovomerine region. Modally, this part of the skull appears as an almost uninterrupted anterior prolongation of the dorsal skull outline, and the vomer tip lies slightly below the level of the parasphenoid. Exceptionally, the ethmovomerine region is decurved, projecting well below the level of the parasphenoid, and the skull has a more convex dorsal profile than that of the modal type. Examples (Fig. 9B) are seen in *P. dentex, P. bayoni* and *P. vittatus.* Intermediate types, however, link the extreme with the modal form.

In the nominate subgenus of *Prognathochromis* (see p. 19), the posterior (*ie* orbital) face of the lateral ethmoid slopes backwards at an angle of 45°–60° with the horizontal; in the other subgenus it is more nearly vertical (75°–80°), the common condition amongst haplochromine lineages. In that subgenus too, the lateral aspects of the bone are more expansive and anteriorly protracted than in the nominate subgenus; again, this is the more usual haplochromine condition.

Characters contributing to the low, slender and streamlined appearance of the skull in *Prognathochromis* (*ie* the shallow preorbital depth, low orbital and otic regions, the low, gently sloping supraoccipital crest, and the narrow otic region) are all derived features, and constitute the principal synapomorphies defining the lineage.

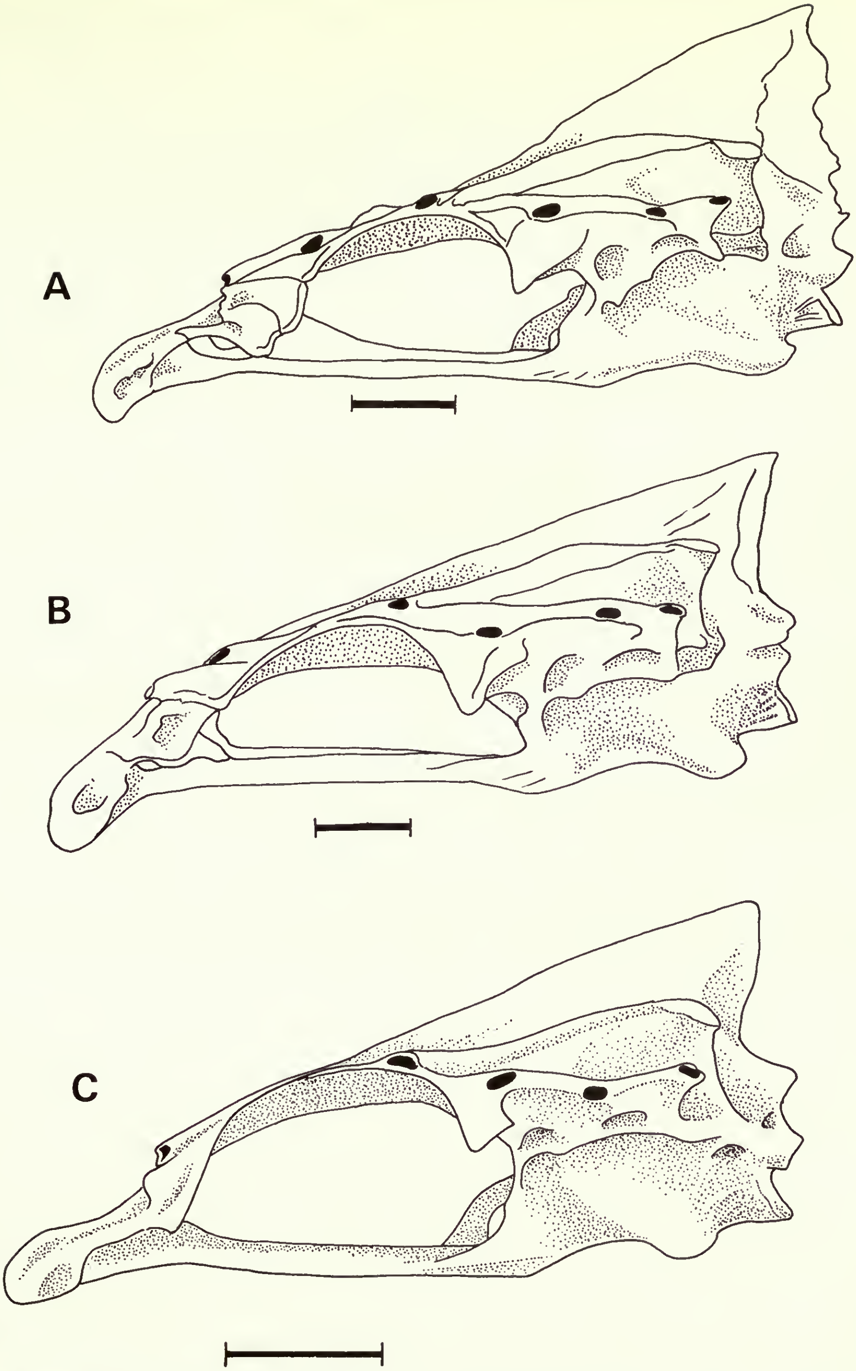

Fig. 9 Neurocranium (in left lateral view) of: A. *Prognathochromis (P.) mento.* B. *Prognathochromis (P.) dentex.* C. *Prognathochromis (T.) sulphureus.* Scale = 5 mm.

Dentition. Specimens over 90 mm SL in most *Prognathochromis* species have a preponderance of strong, recurved, unicuspid teeth in the outer row of both jaws. Some unequally bicuspid teeth may also be present in specimens between 90 and 110 mm SL, but are in a minority, only predominating in fishes less than 80 mm long.

A predominantly unicuspid outer dentition (at least anteriorly in the jaws) also occurs, in some species only, at a length of less than 90 mm. The majority of these species (8 out of 11) belong to a distinct subsdivision of the genus (see p. 20) whose members are further distinguished by the occurrence of tricuspid teeth anteriorly and anterolaterally in the outer tooth row, and by their small adult size (96–120 mm SL). These tricuspid teeth are not simply displaced elements from the inner tooth rows, and their presence is considered a derived feature.

Both subdivisions of *Prognathochromis* have the inner teeth arranged in 2 or 3 rows, exceptionally in a single row or as many as 5 or 6 rows. The teeth are generally tricuspid in fishes < 100 mm SL and unicuspid (or mixed uni- and tricuspids) in larger individuals.

Upper jaw. The premaxilla is always beaked. The degree of this anterior and anterolateral extension of the dentigerous arms shows continuous interspecific variation, but is always noticeable (Fig. 10).

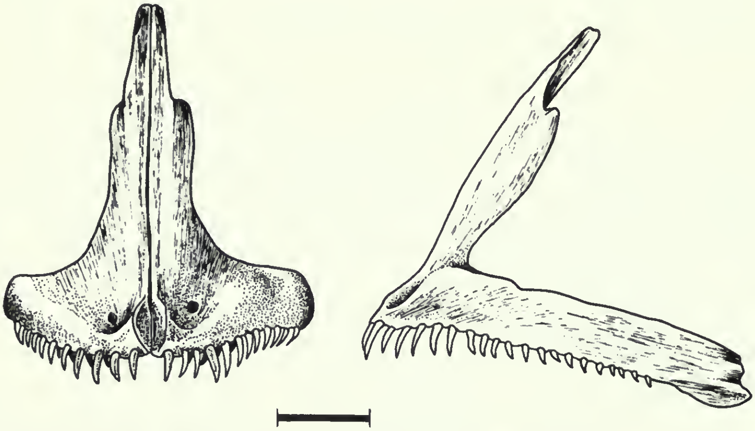

Fig. 10 Premaxilla of *Prognathochromis (P.) argenteus,* seen anteriorly and in left lateral view. Scale = 5 mm.

Lower jaw. In no species is the dentary foreshortened, but there is considerable interspecific variation in the depth of this bone. Most members of the nominate subgenus have a relatively stout (*ie* deep) dentary, but in all species of the other subgenus the bone is noticeably shallower and more slender. In this group too, the lateral aspect of the dentary is deeply concave; when viewed anteriorly, it has a pronounced upward and outward flare and the alveolar surface projects laterally as a distinct shelf (see Greenwood & Barel, 1978 : 155; and Fig. 11).

A prominent mental protuberance at the ventral end of the symphysis is present in both subgenera.

The crown of the ascending (coronoid) dentary arm is always deflected laterally, most obviously so in species of the nominate subgenus, less markedly in the others. The deflection in both subgenera is stronger than in any *Harpagochromis* species.

The insertion point for the mandibulo-interopercular ligament is prominent and well-developed in the nominate subgenus but poorly developed in the other subgenus.

Lower pharyngeal bone and teeth. The dentigerous surface of this bone is triangular, usually as broad as it is long, but sometimes slightly broader than long.

In one subgenus (see p. 20) the lower pharyngeal bone is relatively narrow and its dentigerous surface has an anteroposteriorly attenuate appearance (Fig. 12; and figs 5, 10 and 12 in Greenwood & Barel, 1978). The pharyngeal teeth in this subgenus are finer and more compressed than those of the nominate subgenus, and the teeth in the two median and the posterior transverse row are, relatively speaking, less enlarged.

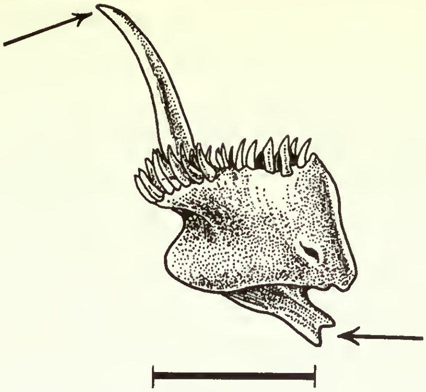

Fig. 11 Anterior view of right dentary in *Prognathochromis (T). dolichorynchus* to show overhang of alveolar shelf, and 'flare' of the dentary's outer wall. Arrows point to: ascending (coronoid) arm of the ramus (upper arrow), and the anterior part of the anguloarticular (lower arrow). Scale = 3 mm.

Vertebral numbers: 28–32 (mode 30), comprising 12–14 (mode 13) abdominal and 15–18 (modes 17 and 18) caudal elements excluding the fused PU_1 and U_1 centra.

Caudal fin. An obliquely truncate fin (see p. 12 above) occurs in some specimens of one species (*P. pseudopellegrini*), but otherwise the fin is truncate or weakly subtruncate.

The two subgenera recognized are:

Subgenus *PROGNATHOCHROMIS* nov.

Type species: *Paratilapia prognatha* Pellegrin, 1904; see Greenwood (1967 : 78).

Diagnosis. *Prognathochromis* without tricuspid teeth in the outer tooth row of either jaw (except, very rarely, as obviously displaced elements from the inner series), usually reaching a large maximum adult size (140–230 mm SL) but only to a length of 93–105 mm in 3 species. First infraorbital (lachrymal) bone with a very slight anterior bullation preceding the anterior infraorbital lateral line tubule, the bullation barely visible without dissection. *Maximum orbital depth of the skull 22–25% neurocranial length (modal range 22–23%). Lateral ethmoid relatively narrow, its posterior face sloping backwards at an angle of 45°–60° to the horizontal.* Lower jaw (especially the dentary) not noticeably shallow, and with a moderately pronounced alveolar shelf visible when the bone is viewed frontally. Lower pharyngeal teeth coarser than those in the other subgenus, the bone itself not distinctly attenuated.

Contained species

Since no intragroup relationships can be determined, the species are listed alphabetically.

Prognathochromis (Prognathochromis) arcanus (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 52–4).

Prognathochromis (*P.*) *argenteus* (Regan), 1922. Lake Victoria; see Greenwood (1967 : 84–7).

Prognathochromis (*P.*) *bartoni* (Greenwood), 1962. Lake Victoria; see Greenwood (1962 : 161–4).

Prognathochromis (*P.*) *bayoni* (Blgr.), 1909. Lake Victoria; see Greenwood (1962 : 149–52).

Prognathochromis (*P.*) *decticostoma* (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 55–7).

Prognathochromis (*P.*) *dentex* (Regan), 1922. Lake Victoria; see Greenwood (1962 : 167–9)

Prognathochromis (*P.*) *dichrourus* (Regan), 1922. Lake Victoria; see Greenwood (1967 : 65–9).

Prognathochromis (*P.*) *estor* (Regan), 1929. Lake Victoria; see Greenwood (1962 : 164–7).

Prognathochromis (*P.*) *flavipinnis* (Blgr.), 1906. Lake Victoria; see Greenwood (1962 : 192–5).

Prognathochromis (*P.*) *gilberti* (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 57–60).

Prognathochromis (*P.*) *gowersi* (Trewavas), 1928. Lake Victoria; see Greenwood (1962 : 180–3).

Prognathochromis (*P.*) *longirostris* (Hilgend.), 1888. Lake Victoria and possibly the Victoria Nile; see Greenwood (1962 : 171–4).

Prognathochromis (*P.*) *macrognathus* (Regan), 1922. Lake Victoria; see Greenwood (1962 : 183–6).

Prognathochromis (*P.*) *mandibularis* (Greenwood), 1962. Lake Victoria; see Greenwood (1962 : 178–80).

Prognathochromis (*P.*) *mento* (Regan), 1922. Lake Victoria; see Greenwood (1962 : 174–8).

Prognathochromis (*P.*) *nanoserranus* (Greenwood & Barel), 1978. Lake Victoria; see Greenwood & Barel (1978 : 157–61).

Prognathochromis (*P.*) *paraguiarti* (Greenwood), 1967. Lake Victoria; see Greenwood (1967 : 69–72).

Prognathochromis (*P.*) *pellegrini* (Regan), 1922. Lake Victoria; see Greenwood (1962 : 186–9).

Prognathochromis (*P.*) *percoides* (Blgr.), 1915. Lake Victoria; see Greenwood (1962 : 189–91).

Prognathochromis (*P.*) *prognathus* (Pellegrin), 1904. Lake Victoria; see Greenwood (1967 : 78–83).

Prognathochromis (*P.*) *pseudopellegrini* (Greenwood), 1967. Lake Victoria; see Greenwood (1967 : 56–60).

Prognathochromis (*P.*) *venator* (Greenwood), 1965. Lake Nabugabo; see Greenwood (1965 : 342–6).

Prognathochromis (*P.*) *vittatus* (Blgr.), 1901. Lake Kivu; see Regan (1921 : 638).

Prognathochromis (*P.*) *xenostoma* (Regan), 1922. Lake Victoria; see Greenwood (1967 : 51–6).

Incertae sedis

Astatotilapia nigrescens Pellegrin, 1909 (Lake Victoria). This taxon, known only from the holotype, has a close superficial resemblance to both *P.* (*P.*) *flavipinnis* and *P.* (*P.*) *percoides* (see Greenwood, 1967 : 118–19). It is for this reason alone that I am including it, tentatively, as a member of this subgenus.

Subgenus ***TRIDONTOCHROMIS*** nov.

TYPE SPECIES: *Haplochromis tridens* Regan & Trewavas, 1928 (see Greenwood, 1967 : 97). Lake Victoria.

ETYMOLOGY. The name alludes to the tricuspid teeth which are a feature of the outer tooth row in both jaws.

DIAGNOSIS. *Prognathochromis* species in which *tricuspid teeth occur anteriorly and anterolaterally* (as well as posteriorly) *in the outer tooth rows of, generally, both jaws;* the size and number of these teeth, together with their inevitable presence, militate against their merely being displaced elements from the inner tooth series. *The lachrymal bone (1st infraorbital) has, in 8 of the 9 species known, an enlarged, ovoid to rectangular bullation occupying the greater part of the bone anterior to the first lateral line tubule, the bulla visible without dissection.* Maximum orbital depth is 23–28% of the neurocranial length (modal range 26–27%), the lateral ethmoid is more expansive than in species of the nominate subgenus, and its posterior face is aligned almost vertically or at an angle of 70°–80° with the horizontal. *The lower pharyngeal bone is narrow, its dentigerous surface having an anteroposteriorly attenuate appearance* (see Fig. 12 and figs 5, 10 & 12 in Greenwood & Barel, 1978); teeth on this bone are fine and compressed. *The lower jaw is shallow, its lateral face having a pronounced upward and outward flare so that the alveolar surface is carried as a prominent shelf overhanging the body of the bone* (see fig. 4 in Greenwood & Barel, 1978).

Members of this subgenus reach a small maximum adult size (95–120 mm SL), becoming sexually mature at a standard length of between *ca* 55–85 mm.

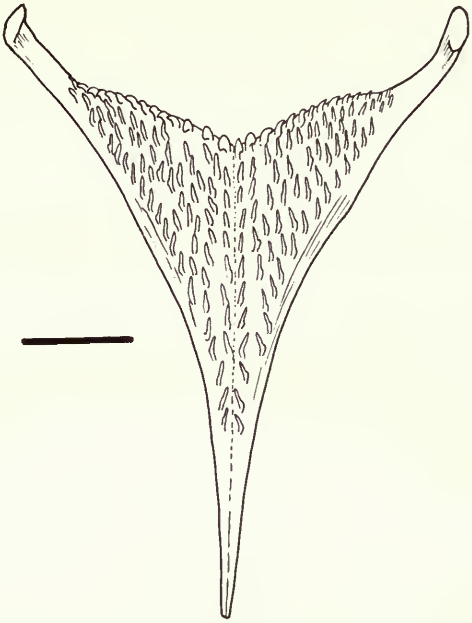

Fig. 12 Lower pharyngeal bone of *Prognathochromis (T.) crocopeplus* in occlusal view. Scale = 2 mm.

Contained species

No intragroup relationships can be determined, and the species are therefore listed alphabetically.

Prognathochromis (*Tridontochromis*) *chlorochrous* (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 44–8).
Prognathochromis (*T.*) *crocopeplus* (Greenwood & Barel), 1978. Lake Victoria; see Greenwood & Barel (1978 : 142–8).
Prognathochromis (*T.*) *cryptogramma* (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 48–51).
Prognathochromis (*T.*) *dolichorhynchus* (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 34–40).
Prognathochromis (*T.*) *melichrous* (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 24–8).
Prognathochromis (*T.*) *plutonius* (Greenwood & Barel), 1978. Lake Victoria; see Greenwood & Barel (1978 : 151–5).
Prognathochromis (*T.*) *sulphureus* (Greenwood & Barel), 1978. Lake Victoria; see Greenwood & Barel (1978 : 148–51).
Prognathochromis (*T.*) *tridens* (Regan & Trewavas), 1928. Lake Victoria; see Greenwood (1967 : 97–100).
Prognathochromis (*T.*) *tyrianthinus* (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 40–4).

Incertae sedis

Haplochromis eutaenia Regan & Trewavas, 1928. The type and only specimen of this species is now rather damaged, particularly about the jaws. As a result the dentary is broken and there are almost no outer series teeth in either jaw. The remaining teeth are bicuspids, but the morphology of the dentary, the overall proportions of the specimen, and what little I can learn about its neurocranial architecture, all suggest that the species could be referred to this subgenus of *Prognathochromis.*

Lake Victoria; see Regan & Trewavas (1928 : 225–6).

DISCUSSION

The characteristic and derived skull form in *Prognathochromis* (see above, p. 16) seems to provide a strong argument for the monophyly of the lineage. Certainly it would be more parsimonious to consider this to be so than to argue that such a distinctive skull form had evolved independently and on several occasions. But, as is so often the case with the Victoria–Edward–Kivu haplochromines, there are few other unequivocally synapomorphic features to back-up the single, diagnostic one.

Again, an absence of synapomorphic characters makes it difficult to identify the sister group of *Prognathochromis.* In an earlier attempt (Greenwood, 1974), certain paedophagous species were tentatively identified as the sister taxon of *Prognathochromis* (then represented by what is now the nominate subgenus).

A more critical analysis of the features on which that suggestion was based, shows that it is no longer tenable; some of the characters involved proved to be plesiomorphies, and others to be autapomorphies.

I have also not been able to find new features that would corroborate my suggestion that *Prognathochromis* and *Harpagochromis* are closely related (Greenwood, 1974). *Prognathochromis* could, on available anatomical evidence, be derived from an *Harpagochromis* or an *Astatotilapia*-like ancestor. However, since in certain respects the skull form in *Harpagochromis* does depart from the generalized *Astatotilapia* type towards that of *Prognathochromis,* there may be grounds for suspecting some relationship between the two lineages. Unfortunately, since there are no other features to support (or negate) this idea, it must remain as no more than a suggestion.

In the same tentative phylogeny (Greenwood, 1974 : fig. 70), the *Tridontochromis* division of *Prognathochromis* was thought to have a rather distant relationship with the nominate subgenus. It was, indeed, allied with a taxon now accorded the status of a monotypic genus, namely *Allochromis welcommei* (see p. 57); the two taxa were, at that time, considered to be the sister group of the *Haplochromis riponianus* complex here included in the genus *Psammochromis,* see p. 53.

First doubts about these proposed relationships were expressed by Greenwood & Barel (1978 : 156), and are confirmed by the research embodied in this paper (see below, p. 60).

For the moment, all that can be established on the basis of synapomorphic characters is the sister-group relationship between the two divisions of *Prognathochromis* itself; their affinities with the other haplochromine lineages from Victoria–Edward–Kivu have still to be discovered.

Intralineage relationships remain indetectable at the level of investigation employed so far. Each subgenus has its morphologically outstanding taxa, but the majority differ from one another only in such features as male coloration and certain morphometric characters.

Within the subgenus *Tridontochromis,* however, *Prognathochromis* (*T.*) *melichrous* stands apart because of the greater number of plesiomorph features it displays, and the skull architecture in all species is less derived than in species of the nominate subgenus. The intralineage dichotomy would seem to have occurred early in the history of the genus.

YSSICHROMIS gen. nov.

TYPE SPECIES: *Haplochromis fusiformis* Greenwood & Gee, 1969. Lake Victoria.

ETYMOLOGY. From the Greek *yssos*, javelin, + *chromis*, alluding to the slender, elongate body form.

DIAGNOSIS. *Shallow bodied, elongate haplochromines (body depth 23–30% SL, modal range 27–29%, caudal peduncle 17–25% of standard length, modal range 19–22%, its depth contained 1·7–2·1 times (modally 1·8–2·0) in its length),* reaching a small maximum adult size (85–110 mm SL).

Neurocranium of the generalized type with a low, wedge-shaped supraoccipital crest. Premaxilla not beaked anteriorly; *edentulous over the posterior* $\frac{1}{4}$–$\frac{1}{3}$ of its dentigerous arms.

Teeth in the outer premaxillary row compressed and unequally bicuspid, those in the dentary similar but with a few tricuspids posteriorly and laterally; 28–64 teeth (no distinct modal number) in the outer row of the premaxilla.

Lower pharyngeal bone slender and elongate, all its teeth fine and compressed.

Lateral line with 32–37 scales (modal range 33–35); cheek fully scaled, with 3 or 4 (rarely 2) rows.

DESCRIPTION

Habitus (Fig. 13). The body is shallow and elongate, the head profile in lateral view moderately acute. Maximum adult size recorded for each of the three constituent species is 110 mm, 93 mm and 85 mm SL respectively.

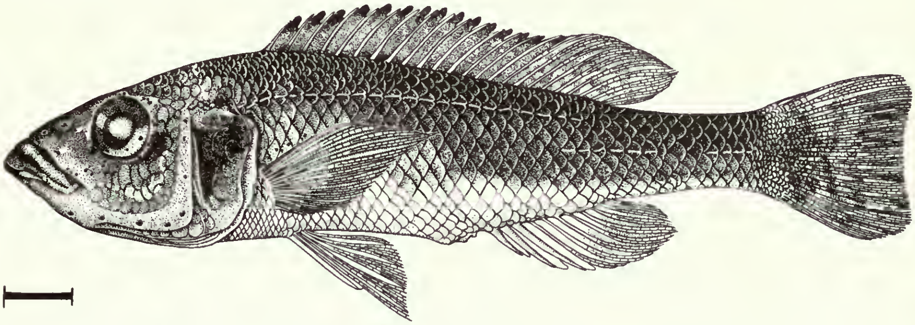

Fig. 13 *Yssichromis fusiformis.* Lake Victoria. Scale = 1 cm.

Superficially, members of this genus resemble those of the *Prognathochromis* lineage, especially members of the subgenus *Tridontochromis.* However, *Yssichromis* species retain several generalized features in the syncranium (see below), and the lower jaw length is shorter, although some overlap does occur (*viz* 35·7–43·8% head length, modal range 40–42% **cf.** 41–62%, modal range 45–53%).

Neurocranium. Neurocranial architecture in this genus is basically of the generalised type (see fig. 18 in Greenwood & Gee, 1969). In one species (*Y. pappenheimi*), however, the preorbital and orbital depths, and the maximum otic width, are reduced and approach the condition found in *Prognathochromis* (which skull-type that of *Y. pappenheimi* also resembles in having a straight rather than a gently curved preorbital skull profile).

The supraoccipital crest in all species is relatively low and wedge-shaped in profile, but it is not as low as that in *Prognathochromis.*

Upper jaw. The premaxilla is not produced anteriorly into a definite beak. Posteriorly over about its last $\frac{1}{4}$–$\frac{1}{3}$ each horizontal dentigerous arm is edentulous in all known specimens of *Y. pappenheimi,* and, apart from the rare exception, is edentulous in the other two species as well.

Lower jaw. The mouth is slightly to moderately oblique (20°–35°), with the tip of the lower jaw not, or but marginally projecting beyond the upper jaw.

The dentary departs but little from the generalized type (and is thus relatively deeper than in *Tridontochromis* species). It does, however, have a well-defined upward and outward flare to the lateral walls when viewed frontally, and in this feature closely approximates to the dentary in *Tridontochromis.* Two of the three species (*Y. pappenheimi* is the exception) have a poorly defined mental protuberance at the symphysis, which is visible in skeletal material but barely detectable in whole fishes.

Dentition. Most outer row teeth in both jaws are compressed and unequally bicuspid; posteriorly in the lower jaw there are often some tricuspid teeth, and tricuspids or unicuspids are sometimes present posteriorly in the upper jaw. Posterior teeth in both jaws are either smaller than those situated anteriorly or may be of approximately the same size, even when unicuspid. (The generalized condition, as seen for example in *Astatotilapia* and some other genera, is for the posterior few teeth to be enlarged.)

Teeth forming the inner row or rows are tricuspid and small.

Lower pharyngeal bone and teeth. The bone is narrow and slender, its dentigerous surface slightly broader than it is long. Two species (*Y. pappenheimi* and *Y. fusiformis*) have the transverse posterior margin of the bone deeply indented so that it is acutely 'V' shaped rather than broadly 'V' shaped (the usual condition in all genera except those with hypertrophied pharyngeal bones, and in the third *Yssichromis* species, *Y. laparogramma*).

All lower pharyngeal teeth are fine, laterally compressed, and weakly cuspidate.

Contained species

Yssichromis fusiformis (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 32–34).

Yssichromis laparogramma (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 28–32).

Yssichromis pappenheimi (Blgr.), 1914. Lakes Edward and George; see Greenwood (1973 : 199–204).

DISCUSSION

Although superficially resembling certain species of *Prognathochromis, Yssichromis* cannot be considered a member of that lineage because it does not share with it any derived features in skull architecture or lower jaw proportions.

Yssichromis is an isolated lineage defined by its autapomorphic features (shallow, elongate body, and posteriorly edentulous premaxilla), but otherwise is of a generalized type.

Within the genus, *Y. pappenheimi* from Lakes Edward and George is apparently the most derived species, judging from its skull shape, and *Y. laparogramma* (Lake Victoria) the most plesiomorphic one; *Y. fusiformis,* also from Lake Victoria, occupies an intermediate position in this morphocline.

PYXICHROMIS gen. nov.

TYPE SPECIES: *Haplochromis parorthostoma* Greenwood, 1967. Lake Victoria.

ETYMOLOGY. From the Greek *pyx* (later form of *pyge*), the rump, an allusion to the rump-like protuberance of the nuchal musculature, and, punningly, to the gnome-like physiognomy of the known species.

DIAGNOSIS. Small relatively deep-bodied and compressed haplochromines (body depth 35–42% SL; maximum adult size 117 mm SL), *with a very oblique lower jaw (sloping upwards at 50°–70° to the horizontal), a sharply concave dorsal head profile, and the dorsal surface of the snout virtually horizontal.* The very characteristic profile of these fishes is contributed to by the bulging anterior portion of the cephalic epaxial musculature (see Fig. 14).

The anatomy of the upper jaw is distinctive (see p. 25).

DESCRIPTION

Habitus (Fig. 14). The external features of *Pyxichromis* are highly characteristic. Considering the small adult size attained, the eye diameter (22–28% head length) is small, especially in comparison with that of certain piscivorous groups (eg *Prognathochromis*

(*Tridontochromis*) species) and in *Astatotilapia* and *Haplochromis*; in contrast, the cheek depth in *Pyxichromis* (24–32% head length) is greater.

Members of the genus are sexually mature at a standard length of *ca* 70 mm, and are not known to exceed a length of 117 mm.

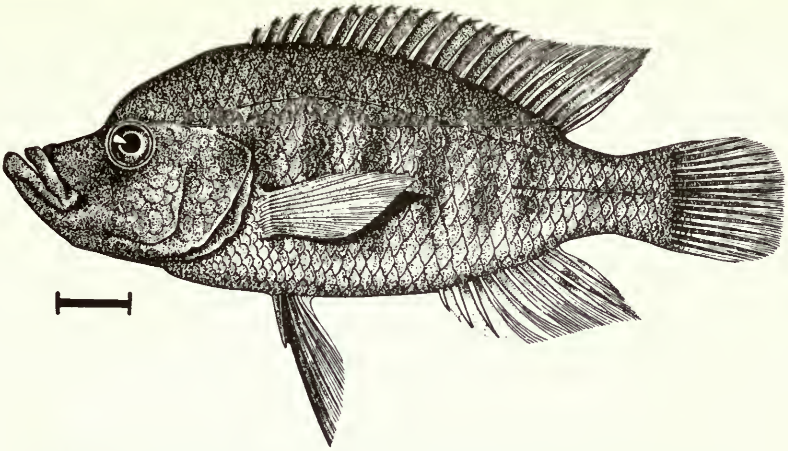

Fig. 14 *Pyxichromis parorthostoma.* Lake Victoria. Scale = 1 cm.

Anatomy. Unfortunately, very few *Pyxichromis* specimens are available and consequently knowledge of its anatomy and osteology is confined to information gleaned from partial dissections and from radiographs.

Neurocranium. Skull form is essentially of the *Astatotilapia* type except that the supraoccipital crest is relatively more expansive, a probable correlate of the somewhat hypertrophied nuchal muscle mass.

Upper jaw. An unusual feature of *Pyxichromis* is the near-horizontal alignment of the dorsal snout surface. Amongst other members of the Victoria–Edward–Kivu haplochromine complex the snout profile slopes downwards and forwards, albeit at various angles, but it is never horizontal. The angle at which the snout descends in these other species virtually parallels the slope of the underlying ethmovomerine region of the skull.

In *Pyxichromis* the ethmovomerine region slopes at almost the same angle as it does in the skulls of *Harpagochromis* and *Prognathochromis* species. That the upper snout profile is, nevertheless, horizontal in *Pyxichromis* can be explained by the hypertrophy of certain articulatory menisci and other surfaces associated with the maxillae and premaxillae.

For example, the median rostral cartilage is much deeper than it is in other taxa, and its ventral face (which is apposed to the sloping ethmovomer) is angled so that its dorsal surface (in contact with the premaxillary process) lies horizontally, not sloping forward and downward as it would otherwise do if the anterior part of the cartilage were not deeper than the posterior part. The premaxillary processes are thus elevated above the ethmovomerine surface and, since the upper surface of the cartilage is almost horizontal, held horizontally as well.

As a result of this arrangement there is a considerable gap anteriorly between the processes and the rostral part of the dorsal ethmoid surface. The premaxillary processes are supported in this region by an hypertrophy of the membrane and cartilage cushion surrounding the condyle of the medially directed posterior process on the maxillary head (the neurocranial process of Barel *et al.,* 1976). More support is derived from the enlarged cushion of tissue capping the anteroventral process of the maxilla (Barel *et al*'s 'premaxilliad wing').

Thus, when the mouth is closed, the premaxilla is supported, and held away from the ethmovomer, by enlarged articulatory points at three places: posteriorly by the rostral cartilage, near its midpoint by the neurocranial process, and anteriorly (where the ascending processes join the body of the bone) by a pad of tissue on the premaxilliad wing of the maxilla.

The alignment and relative enlargement of these three surfaces is such that the premaxillary processes lie almost horizontally, despite the forward and downward slope of the ethmoid and vomer against which two of them articulate.

Lower jaw. As far as I can determine from limited dissections and from radiographs, the lower jaw is not unusual (although I suspect that there are some specialized features in the anguloarticular-quadrate joint). When compared with similar-sized specimens of species belonging to the non-piscivorous lineages (especially *Astatotilapia*), the lower jaw in *Pyxichromis* is somewhat longer (48–57% head length). This is a derived feature shared with both *Harpagochromis* and *Prognathochromis* (see pp. 10 & 16). The jaw is narrow (its maximum width contained more than twice in the length), a correlate of the generally compressed body-form.

Dentition. In fishes >70 mm SL, the outer teeth are mostly slender and unicuspid, but there are interspecific differences in tooth shape and orientation. Only one smaller fish is known (a 67·5 mm SL specimen of *P. orthostoma*); anteriorly and anterolaterally in the upper jaw its outer teeth are bicuspid (as they are throughout the lower jaw) but are short and tricuspid laterally and posterolaterally. With only one small specimen known, the significance of these tricuspid outer teeth cannot be evaluated.

Lower pharyngeal bone and teeth. These are virtually identical with those of *Harpagochromis* and *Prognathochromis* (see p. 18).

Caudal fin. One species (*P. orthostoma,* Lake Kioga system) has a truncate fin, the other species (*P. parorthostoma*; Lake Victoria) has the fin strongly subtruncate, almost rounded.

Contained species

Pyxichromis orthostoma (Regan), 1922. Lake Salisbury, Kioga system; see Greenwood (1967 : 100–2).

Pyxichromis parorthostoma (Greenwood), 1967. Lake Victoria; see Greenwood (1967 : 103–5).

DISCUSSION

Because of its peculiar autapomorphic features, and within the limits imposed by inadequate anatomical and osteological data, it is particularly difficult to assess the affinities of *Pyxichromis.*

Its high relative jaw length, especially in a species with a small maximum adult size, suggests a possible relationship with *Harpagochromis* and *Prognathochromis.* As far as can be told, neurocranial form in *Pyxichromis* is of the near-generalized type and like that found in *Harpagochromis* (see p. 11). Except for the narrow otic region, the neurocranium shows none of the derived features characterizing the skull of *Prognathochromis* (*ie* low preorbital skull depth, low orbital depth, and a relatively shallow, gently sloping supraoccipital crest).

Pyxichromis does, however, share with *Prognathochromis* the derived features of a unicuspid dentition in small individuals, the presence of some tricuspid outer teeth laterally in the jaw (at least in one specimen, the smallest known) and, of course, a relatively, long lower jaw.

LIPOCHROMIS Regan, 1920

TYPE SPECIES: *Paratilapia obesus* Boulenger, 1906. Lake Victoria; for details of synonymy *etc,* see Greenwood (1959*b* : 182–3).

DIAGNOSIS. Haplochromine fishes with an adult size range of 130–170 mm SL, and a varied body form (see Figs 15A & B). All are characterized by having a thick-lipped, *widely distensible and protractile mouth, and small teeth deeply embedded in the oral mucosa (often invisible without dissection).*

The nominate subgenus is characterized by many of its outer row jaw teeth having the crowns reflected labially (not buccally as is usual), *and by its broadly rounded lower jaw. The* *other subgenus is recognizable by its peculiarly boat-shaped lower jaw which narrows abruptly over about its anterior third so that this part of the jaw closes within the upper jaw;* no outer row jaw teeth have their crowns curved labially, and are either erect or recurved.

The neurocranium is essentially of the generalized type, but does have a relatively tall and expansive supraoccipital crest which is near-pyramidical in lateral outline.

DESCRIPTION

Habitus (Fig. 15). Body form is variable, especially with regard to the head and snout profiles; these range from heavy and blunt ('pug-headed'), to slender and subacute (see Figs 15A & B respectively). Body depth ranges from 27–47% of standard length, with some species (as currently defined) showing considerable intraspecific variation (eg 33–47% in *L. obesus,* and 32–43% in *L. maxillaris*). In general, deep-bodied species are pug-headed, and slender bodied ones have a more refined profile.

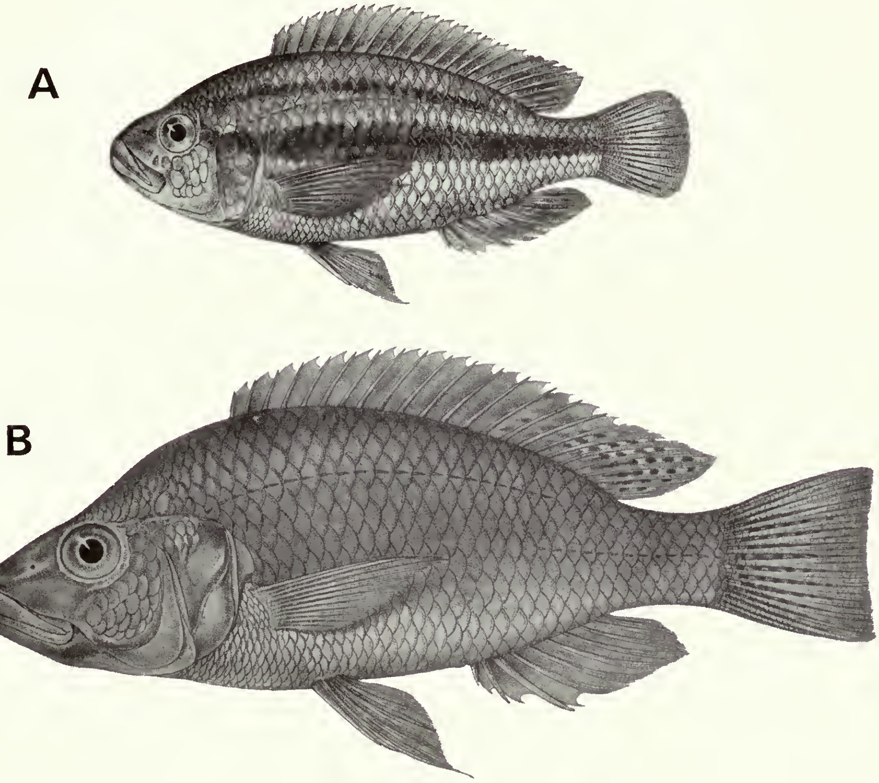

Fig. 15 A. *Lipochromis (Lipochromis) obesus.* Lake Victoria. About two-thirds natural size. B. *Lipochromis (Cleptochromis) parvidens.* Lake Victoria. About two-thirds natural size.

Maximum adult size ranges from 130–170 mm SL, with sexual maturity reached at between 85 and 105 mm SL depending on the maximum adult size for a particular species.

Neurocranium. Basically, the skull is of the near-generalized type found in species of the *Harpagochromis* group (see p. 11) but it retains the deeper otic region of the more generalized skull (see Greenwood, 1974 : fig. 45, excluding skull of *H. barbarae*).

As in *Harpagochromis,* the supraoccipital crest in *Lipochromis* species is high, with a near-pyramidical profile, but it is more expansive than in the majority of *Harpagochromis* species.

Greatest departure from the modal *Lipochromis* skull type is seen in *L. obesus,* where the orbital depth is greater and consequently the preorbital skull profile slopes at a greater angle.

Dentition. All jaw teeth are deeply embedded in the thickened oral mucosa so that, at most, only the crowns of the teeth are visible; often the inner rows are completely buried.

Two distinct forms of outer teeth are present. In one, the tip of the crown is inclined anteriorly or laterally (see below) whilst in the other it is either vertical or fairly strongly recurved (*ie* directed buccally; see below p. 31).

Most outer row teeth in fishes between 70 and 100 mm SL are weakly bicuspid (with, in certain species, some unicuspids and weakly bicuspids also present); above that size the majority of teeth are unicuspid, although in one species (*L. taurinus*) bicuspids predominate even in the largest individuals (see Greenwood, 1973 : 194).

The inner rows, usually 1 or 2, are composed of tricuspid teeth (with a few unicuspids) in fishes <80–100 mm SL, and predominantly of unicuspids in larger individuals.

Compared with the teeth in equal-sized specimens from other lineages, those of *Lipochromis* are shorter (as little as half the height of teeth in members of the piscivorous lineages *Harpagochromis* and *Prognathochromis*); teeth in *Lipochromis* are also often finer (although in some species they are stouter) than in species of the latter genera.

Modally, the total number of teeth in the outer row of the premaxilla is less than in comparable-sized specimens of *Harpagochromis* and *Prognathochromis,* the number ranging from 30–62, but generally about 40. A comparable reduction in the number of outer teeth in the dentary is also noted in *Lipochromis.*

Most individuals in certain species have almost the posterior third of the premaxilla devoid of teeth; when premaxillary teeth are present posteriorly in these taxa, they are widely spaced, as they are in those species with a completely toothed premaxilla.

Lip tissue is well-developed in all species, and the inner aspect of the upper lip is so arranged that it generally covers, or partly covers, the tips of the outer teeth in the upper jaw.

Mouth. The mouth is a very distinctive feature in all *Lipochromis* species, in particular the wide lateral gape of the upper jaw in a fully-opened mouth; in one subgenus this distensibility of the upper jaw is combined with a marked protrusibility.

In all species the lips are thickened, but the bullate posterior end of the maxilla is obvious, even when the mouth is closed.

The orientation of the mouth is slightly oblique in most species, more obviously so in one (*L. microdon*). The lower jaw may project a little way beyond the upper jaw, particularly in those species with an acute head profile.

Relative lower jaw length in *Lipochromis* (38–56% of head length, modal range 42–48%) overlaps that in *Harpagochromis* and *Prognathochromis,* but modally it is shorter. Similarly, its length range overlaps that of most other lineages but in these instances the mode for *Lipochromis* is somewhat higher.

Upper jaw. Posteriorly the maxilla is markedly bullate, its lateral face convex and the inner face concave. The ventral margin over the entire bone, except in the bullate region, is distinctly thickened. Some variation exists in the degree to which the anterior half of the bone is incurved relative to the posterior portion; in most species the curvature is very noticeable, especially so in members of the nominate subgenus (see below, p. 30).

A prominent feature of the premaxilla is the stoutness of its dentigerous arms, which are almost cylindrical in cross-section over the greater part of their lengths. The ascending processes are either as long as the dentigerous arms or are distinctly shorter, a feature positively correlated with the degree of mouth protrusibility.

Lower jaw. The dentary is bullate in the region surrounding its bifurcation into ascending (coronoid) and horizontal arms. This horizontally directed, dorsoventrally compressed swelling is produced forward for almost half the anterior length of each ramus as a thick, shelf-like lateral projection.

The tip of the ascending process has a definite, but interspecifically variable, deflection laterally. A similar deflection occurs in *Prognathochromis,* particularly in members of its nominate subgenus, but in no species is it so noticeable as it is in most *Lipochromis* species. The insertion for the mandibulo-interopercular ligament is prominent and well-developed (to a level comparable with that in *Prognathochromis* (*Prognathochromis*) species).

Two extreme forms of lower jaw morphology are found amongst *Lipochromis* species (see Fig. 16). In one (the *obesus* type) the anterior margin of the jaw is broadly rounded (most clearly so in *L. obesus*); when viewed from below, the alveolar surface appears as a broad shelf projecting above and beyond the ventral half of each ramus, the lateral wall of which is sharply angled towards the midline.

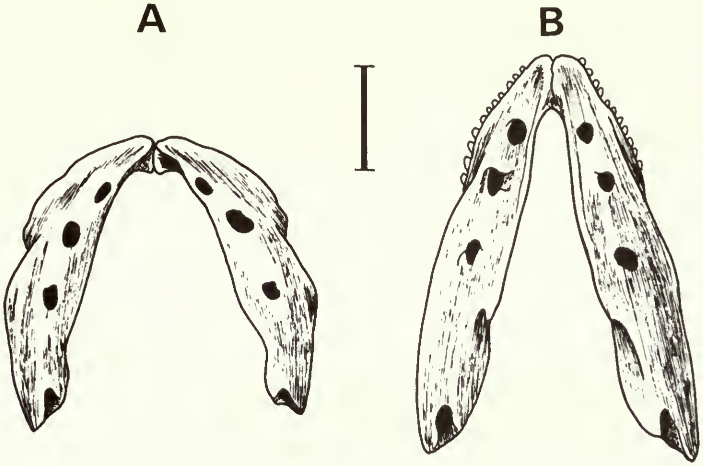

Fig. 16 Dentary in ventral view, of: A. *Lipochromis (L.) obesus*, and B. *Lipochromis (C.) parvidens*. Scale = 5 mm.

In the second, or *parvidens* type, the entire forward portion of the lower jaw anterior to the dentary bifurcation narrows rapidly; the alveolar 'shelf' is thus much less obvious and the anterior jaw outline is more acute (Fig. 16B). Also, since the ventral half of each ramus is, as it were, pinched medially, this anterior narrowing is emphasized and the ventral contours of the rami are rounded. In section, the jaw is rather boat-shaped, especially when viewed from in front. (In nautical terms, the shape is like that of a pram seen bow-on.)

Although the extreme conditions, as represented by *L. obesus* and *L. parvidens*, are very distinctive, some species have a jaw shape that almost bridges this morphological gap (see, for example, the lower jaws in *L. maxillaris* and *L. cryptodon*; Greenwood, 1959 : 189, 192 & 198–200).

Lower pharyngeal bone and dentition. The bone is broad and short, its dentigerous surface triangular and as broad as, or more often, broader than it is long. The teeth are fine and weakly bicuspid, with only those of the posterior transverse row, and some posteriorly in the two median rows, coarser than the others.

Taking into account the differences in dentition and in jaw morphology, it would seem that intragroup relationships of *Lipochromis* are best expressed by recognizing two subgenera. This action reflects and corrects an earlier view (Greenwood, 1974) that the paedophage trophic radiation (here represented by the genus *Lipochromis*) was of diphyletic origin. Further consideration of that idea has led me to give greater phylogenetic emphasis than before to the derived features shared by all *Lipochromis* species (*viz* buried teeth reduced in size and number, coupled with great distensibility and protrusibility of the upper jaw), and to the lack of characters suggesting an alternate relationship for any or all of the species involved. Hence, the recognition of one lineage comprising two subdivisions.

Subgenus ***LIPOCHROMIS*** Regan, 1920

TYPE SPECIES: *Pelmatochromis obesus* Blgr., 1906 (see Greenwood, 1959*b* : 182–8).

Members of this subgenus are characterized by the presence, in *the outer tooth row, of stout uni- or bicuspid teeth whose crowns are inclined labially (*ie *anteriorly or laterally depending* *on their position in the jaw).* Such teeth (Fig. 17) usually are the predominant type in the lower jaw; if present in the upper jaw they are intercalated amongst the more numerous recurved (*ie* buccally directed) or erect and conical teeth. Bicuspid teeth are the commonest type in fishes < 100 mm SL, but in one species (*L. taurinus* from Lakes Edward and George) most teeth are bicuspid even in specimens 140 mm long. Compared with the teeth in members of the other subgenus, those in *Lipochromis* are stouter and shorter.

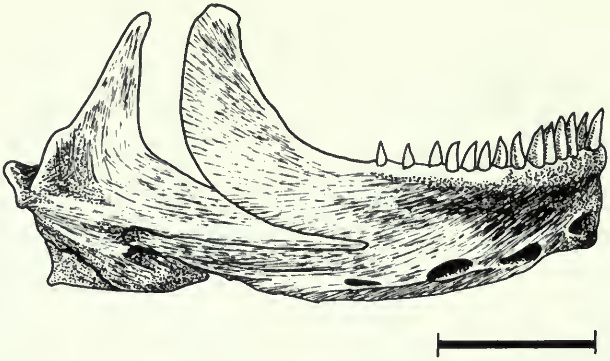

Fig. 17 Dentary (right) of *Lipochromis (L.) obesus* to show labial curvature of certain outer row teeth. Scale = 5 mm.

The lower jaw, save in one species, is of the *obesus* type (see above, and Fig. 16A), although in the majority of species it is not as broad anteriorly as it is in *L.* (*L.*) *obesus* itself. With the same exceptional species, the lower jaw does not close within the upper. The exception, *L.* (*L.*) *melanopterus,* was known only from the holotype; however, material collected recently in Lake Victoria indicates that it is not, as once was thought, an aberrant specimen (see Greenwood, 1959*b* : 192–4). As far as could be determined from superficial examination, radiographs and limited dissection on the holotype, the dentary in *L.* (*L.*) *melanopterus* is essentially of the *parvidens* type (see above p. 29) a conclusion confirmed from the examination of new material. In its dentition, head shape and oral features, however, *L.* (*L.*) *melanopterus* is typically a member of the nominate subgenus.

Regan's (1920) original description of *Lipochromis* (based solely on the species *obesus*) gave as the only diagnostic feature '. . . Lower jaw shutting within the upper'. The type specimen of *Pelmatochromis obesus,* the only specimen available at that time, is very atypical and also rather poorly preserved. Certainly the lower jaw does seem to shut within the upper, but in my view this is more likely to be a preservation artefact than the natural condition (see also Greenwood, 1959*b* : 183). In none of the 47 other specimens on which my redescription of the species was based does the lower jaw fail to occlude with the upper.

Species of *Lipochromis* (*Lipochromis*) have a 'pug-headed' morphotype unlike the more elegant head form in all known species of the second subgenus.

The mouth is moderately protractile but is markedly distensible laterally. The premaxillary ascending processes are much shorter than the dentigerous arms of the bone (even in *L.* (*L.*) *melanopterus*), hence, presumably, the comparatively restricted protusibility of the upper jaw.

Contained species

The taxa are listed in order of their apparently increasing level of derivation.

Lipochromis (*Lipochromis*) *taurinus* (Trewavas), 1933. Lakes Edward and George; see Greenwood (1973 : 192–6).

Lipochromis (*L.*) *maxillaris* (Trewavas), 1928. Lake Victoria; see Greenwood (1959*b* : 189–192).

Lipochromis (*L.*) *obesus* (Blgr.), 1906. Lakes Victoria and Kwania (Uganda); see Greenwood (1959*b* : 182–8).
Lipochromis (*L.*) *melanopterus* (Trewavas), 1928. Lake Victoria; see Greenwood (1959*b* : 192–4).

Subgenus ***CLEPTOCHROMIS*** nov.

TYPE SPECIES: *Paratilapia parvidens* Blgr., 1911. Lake Victoria (see Greenwood, 1959*b* : 194–8).

ETYMOLOGY. From the Greek *kleptes*, a thief, + *chromis*, with reference to the paedophagous habits of its member species.

Species of this subgenus are characterized by the unusual form of the dentary, and by the outer row of jaw teeth being mainly slender, recurved, often strongly recurved unicuspids in specimens over *ca* 100 mm SL, and weakly recurved bicuspids in smaller fishes; in no species are there any teeth with anteriorly or laterally directed crowns (**cf.** subgenus *Lipochromis*).

The lower jaw, at least anteriorly, closes within the upper, and has a boat-shaped dentary of the 'parvidens' type (see above p. 29 *and* Fig. 16B*). The mouth is both markedly distensible and protractile.*

In all known species the ascending premaxillary processes are as long as, or longer than the dentigerous arms of that bone.

Contained species
The taxa are arranged in their apparently increasing order of derivation.
Lipochromis (*Cleptochromis*) *cryptodon* (Greenwood), 1959. Lake Victoria; see Greenwood (1959*b* : 198–200).
Lipochromis (*C.*) *microdon* (Blgr.), 1906. Lake Victoria; see Greenwood (1959*b* : 200–3).
Lipochromis (*C.*) *parvidens* (Blgr.), 1911. Lake Victoria; see Greenwood (1959*b* : 194–8).

DISCUSSION
The genus *Lipochromis* comprises two groups of embryonic and larval cichlid-eating haplochromines (the paedophages) discussed in Greenwood (1959*b* & 1974 for the species of Lake Victoria) and 1973 for the Edward–George species. They are now united in a single lineage because of their presumed synapomorphies, namely: jaw teeth deeply embedded in the thickened oral mucosa, the teeth reduced in size (relative to those in comparable sized specimens from other lineages) and often absent from the posterior part of the premaxilla, the mouth widely distensible (through a mechanism effecting a marked lateral displacement of the upper jaw moieties when the mouth is opened), a highly protrusible premaxilla, the pronounced bullation of the posterior maxillary arm, and the thickened ventral margin of the maxilla.

There are two other derived characters shared by all members of this lineage: the premaxillary dentigerous arms are inflated, and the dentary is greatly swollen posteriorly in the region of its bifurcation into ascending and horizontal arms. However, there is evidence indicating that these features could be the result of convergent trends associated with the evolution of a jaw that is much involved in the handling of prey objects. Probably in the case of *Lipochromis* those jaw features are truly synapomorphic, but since the possibility of their convergent evolution in other genera exists, they are unreliable indicators of any relationship between *Lipochromis* and lineages showing the same features (see discussions on pp. 52, 71 & 75).

Previously (Greenwood, 1974) I postulated a diphyletic origin for the paedophage trophic radiation. Some of the cranial characters on which that argument was based are now seen to be plesiomorphous, and the dental features used are probably associated with the large adult size attained by the paedophage species. Thus, there seem to be no adequate grounds for suggesting that *Lipochromis* might share a recent common ancestry with *Harpagochromis* and *Prognathochromis* (the lineages in which most of the species linked with the paedophages in my earlier analysis are now placed; see Greenwood, 1974, fig. 70 and discussions in the text). Indeed, I can find no unequivocally apomorph features that would allow one reasonably to identify the sister group of *Lipochromis.*

Two paedophage (or partly paedophagous) species, *'H' cronus* and *'H' barbarae* were formerly associated with, respectively, the '*obesus*' and '*parvidens*' lineages recognized by Greenwood (1974). Since neither of these species has any of the synapomorphic features characterizing *Lipochromis,* neither is currently included in *Lipochromis* (see p. 8 and p. 88 for *'barbarae'* and *'cronus'* respectively; also Barel, Witte & van Oijen (1976) for a comparative anatomical study of the palate in *'H' barbarae* and various *Lipochromis* species).

Within the *Lipochromis* lineage it is only possible to note that, for the species so far described, *L.* (*L.*) *taurinus* from Lake Edward and George has the least derived dental morphology for taxa in its subgenus, and that *L.* (*C.*) *parvidens* shows the greatest jaw distensibility and tooth reduction amongst members of its subgenus.

When the several species recently collected in Lake Victoria are studied further it may be possible to produce a more satisfactory indication of intralineage relationships (personal observations based on material collected by the Leiden University research team).

GAUROCHROMIS gen. nov.

Type species: *Haplochromis empodisma* Greenwood, 1960. Lake Victoria.

Etymology. From the Greek '*gauros*', haughty + *chromis,* alluding to the physiognomy in at least four of the member species.

Diagnosis. Deep to relatively deep-bodied haplochromines (body depth 30–44% SL, modal range 38–39%), with a straight or slightly concave but steeply sloping dorsal head profile interrupted by the prominent ascending process of the premaxilla. Mouth horizontal or slightly oblique, lips not thickened, and the teeth small, fine and numerous but rarely contiguous.

Premaxilla with compressed (*ie* not inflated) dentigerous arms that are longer than the ascending processes, and which are not produced anteriorly into a beak or shelf.

Outer teeth in both jaws (particularly when compared with those in Labrochromis and *Astatotilapia) finer, more compressed, shorter and closer set, with 44–82 (modal range 60–70) in the premaxillary outer row.* Fishes <90 mm SL have unequally bicuspid teeth (the major cusp acutely pointed but sometimes obscured by a dark brown accretion), *the crown barely broader than the neck.* Larger fishes have a mixed dentition of weakly bicuspid and unicuspid teeth, the latter predominating in the largest specimens. An exclusively unicuspid outer dentition has never been recorded.

Inner row teeth small, generally tricuspid, and arranged in 1 or 2 (less frequently 3) rows anteriorly and laterally in both jaws; separated from the outer row by a distinct space.

Two kinds of lower pharyngeal bone occur. One is slender, narrow and relatively elongate, with all or the majority of its teeth fine and compressed. A few teeth in the two median rows may be coarser than the others, but none is molariform or submolariform.

The second type of lower pharyngeal bone is distinctly hypertrophied and stout, and has thick, short, articular horns. The two median tooth rows are composed of enlarged and molariform teeth, and usually there are several other rows containing enlarged and submolariform (or even molariform) teeth. Fine, compressed and distinctly unicuspid teeth are virtually confined to the posterolateral angles of the dentigerous surface.

Description

Habitus (Fig. 18). Although not particularly deep-bodied (depth 30–44% SL, modal range 38–39%) the total impression gained from a specimen of *Gaurochromis* is one of a deep-bodied fish. The premaxillary ascending processes are prominent and break the outline of steeply sloping dorsal head profile, giving the fish a distinctive 'Roman nose'. The lips are not thickened, and the mouth is horizontal or slightly oblique.

The maximum adult size range is 90–117 mm SL.

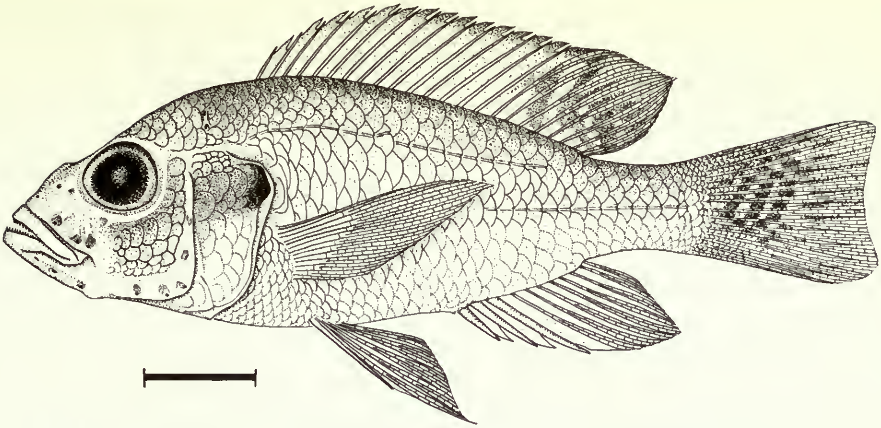

Fig. 18 *Gaurochromis (Gaurochromis) angustifrons.* Lake George. Scale = 1 cm.

Neurocranium Skull architecture is of the generalized type, with a straight and moderately sloping dorsal profile; preorbital depth ranges from 19–27% neurocranial length (being lowest in *G. angustifrons* from Lakes Edward and George), the mode lying in the lower part of the range for taxa with a generalized skull type. The height of the supraoccipital crest varies from low to relatively low, the bone being wedge-shaped in lateral profile.

In some species the neurocranial apophysis for the upper pharyngeal bones is hypertrophied (see p. 36).

Dentition. Teeth in both jaws are fine, slender and compressed. Those in the outer row are slightly recurved and, especially in the anteroposterior dimensions of the crown, noticeably finer than the teeth in similar-sized specimens from other taxa; in general these teeth are also shorter.

Most outer teeth in fishes <90 mm SL have the generalized type of unequally bicuspid crown which is marginally broader than its subcylindrical neck; the major cusp is acutely pointed. Some slender, compressed unicuspids may be present in fishes less than 90 mm long, and weakly bicuspid teeth may also occur. The latter are the predominant teeth in larger fishes. An entirely or even a mainly unicuspid outer dentition has not been recorded in large individuals (*ie* >100 mm SL) of any *Gaurochromis* species (see Greenwood, 1960 : 264; 1965 : 326; 1973 : 180).

The outer teeth are close-set but rarely contiguous, with 44–82 (modal range 60–70) in the premaxilla. Although the range overlaps that of *Astatotilapia, viz* 34–74 (and thus the presumed primitive numbers), the modal range is higher in *Gaurochromis* (60–70 **cf.** 48–54).

Inner row teeth are small and usually tricuspid, but some weakly tricuspid and even unicuspid teeth may be present in fishes > 100 mm SL. The teeth in both jaws are arranged in 1 or 2 (less commonly 3) rows anteriorly and anterolaterally, and a single row posteriorly.

Upper jaw. The maxilla is slender and elongate, its articular head with a fairly marked medial curvature relative to the shaft of the bone.

The dentigerous arms of the premaxilla are compressed, and are longer than the ascending processes. Anteriorly, the bone is not produced into a shelf or beak.

Lower jaw. In two species (*G. empodisma* and *G. simpsoni*) the dentary is slender and relatively shallow, its alveolar surface produced laterally into a narrow but distinct shelf; in the third species (*G. angustifrons*), the shelf is less obvious but is nevertheless clearly defined, more so than in the generalized condition.

The lower jaw length is 38–49% head (modal range 41–44%) thus overlapping the range in the generalized taxon *Astatotilapia* and in other but trophically specialized non-piscivorous lineages; however, the upper part of its range exceeds that in those taxa, and the modal range is also higher.

Lower pharyngeal bone. Two distinct types of lower pharyngeal bone (with correlated differences in the upper bones) occur in *Gaurochromis.*

In one type (Fig. 19) the bone is slender and narrow, with a long anterior shaft and fine, elongate articular horns. Its dentigerous area is attenuated, the lateral margins narrowing rapidly to produce an outline which is nearer that of an isosceles than an equilateral triangle. This overall attenuation is seen most clearly when the bone is superimposed onto one from a similar-sized specimen of some other lineage, for example, any species of *Astatotilapia.*

There is some intrageneric variation in the degree of attenuation, with the bone in *G. angustifrons* being the narrowest and most attenuated (see Greenwood, 1973 : fig. 19).

The lower pharyngeal teeth are fine, slender, and compressed, with weakly cuspidate and not greatly protracted crowns; even those teeth forming the posterior transverse row are strongly compressed so that they do not appear to be relatively enlarged (as is the case in most other lineages). Teeth forming the median rows are sometimes slightly coarser than their lateral counterparts, but none can be described as enlarged.

Except in the posterolateral angles of the bone, the teeth are not densely arranged; consequently the occlusal surface does not have the appearance of a fine dental felt.

The other type of lower pharyngeal bone (and dentition) differs markedly from the slender, attenuate bone described above (Fig. 20). It is moderately hypertrophied and stout (almost massive in some specimens), thus in many respects resembling the type of bone found in the genus *Labrochromis* (see p. 40).

At least the two median rows (and often the two rows lateral to them as well) are composed of enlarged and molariform teeth. In *Gaurochromis obtusidens* nearly all the other teeth are somewhat enlarged, with molariform or submolariform crowns, only those in the posterolateral angles of the bone being distinctly finer and cuspidate.

There appears to be a related species (currently undescribed) in which the bone is less massive and has fewer enlarged and molariform teeth outside the median series.

Neither *Gaurochromis obtusidens,* nor the undescribed species have the entire bone or its dentigerous surface so characteristically attenuated as it is in the other species. Yet, when compared with *Labrochromis,* the bone is narrower relative to its length (Fig. 21) and the dentigerous area is more nearly isoscelene than equilateral. Also, the articular horns, though stouter than in the other *Gaurochromis,* are neither as short nor as massive as those in *Labrochromis.*

Based on these intralineage differences in pharyngeal bone morphology and dentition, two divisions of *Gaurochromis* are recognised, each characterized by its autapomorphic features.

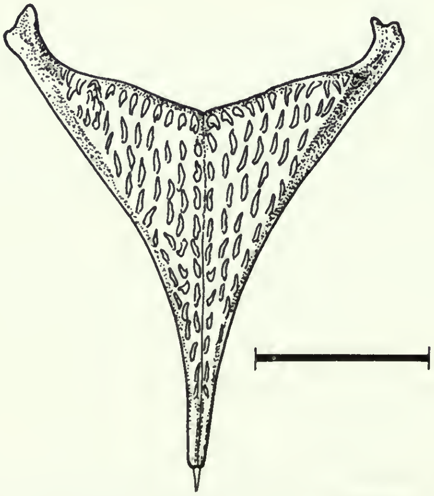

Fig. 19 Lower pharyngeal bone of *Gaurochromis (Gaurochromis) simpsoni,* in occlusal view. Scale = 3 mm.

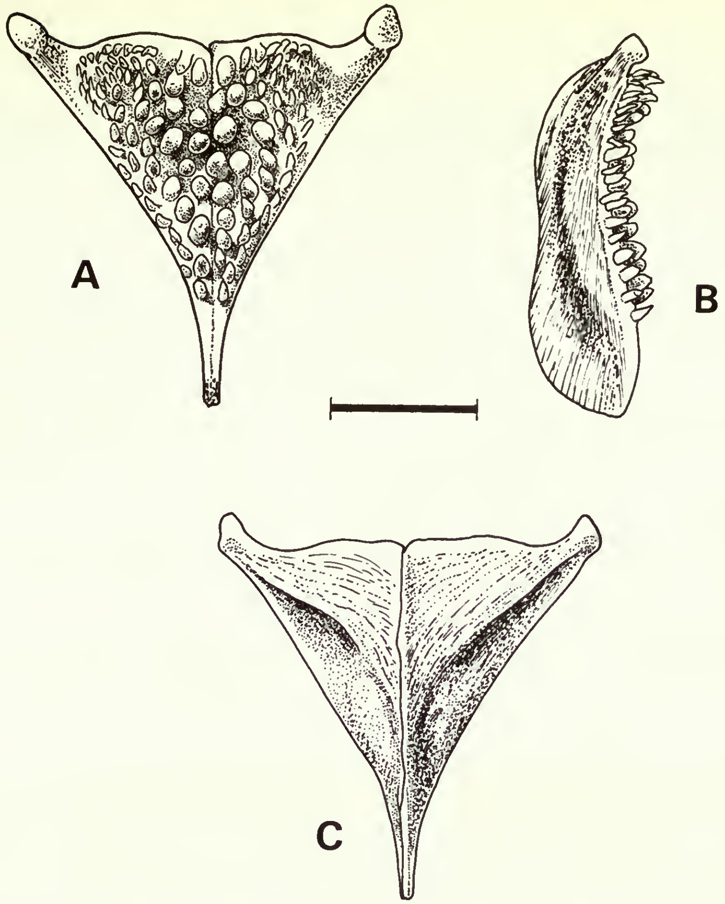

Fig. 20 Lower pharyngeal bone of *Gaurochromis (Mylacochromis) obtusidens* in: A. Occlusal. B. Right lateral. C. Ventral view. Scale = 5 mm.

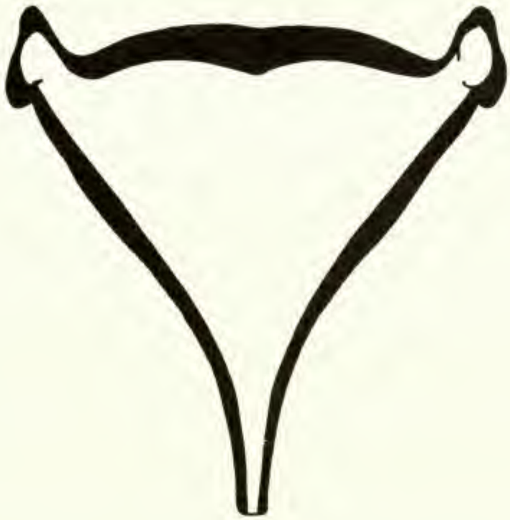

Fig. 21 Outline of lower pharyngeal bone, in occlusal view, of *Gaurochromis (Mylacochromis) obtusidens* (white) superimposed on that of *Labrochromis ishmaeli* (in black). Both bones are from adult specimens of the same standard length.

Subgenus ***GAUROCHROMIS*** nov.

TYPE SPECIES: *Haplochromis empodisma* Greenwood, 1960. Lake Victoria.

DIAGNOSIS. *Gaurochromis* species with a *slender, attenuated and fine lower pharyngeal bone* without molariform lower pharyngeal teeth. The dentigerous area of the bone is narrower than it is long.

Contained species
Gaurochromis (*Gaurochromis*) *empodisma* (Greenwood), 1960. Lake Victoria; see Greenwood (1960 : 262–6).
Gaurochromis (*G.*) *simpsoni* (Greenwood), 1965. Lake Nabugabo; see Greenwood (1965 : 325–9).
Gaurochromis (*G.*) *angustifrons* (Blgr.), 1914. Lakes Edward and George; see Greenwood (1973 : 177–83).

Subgenus ***MYLACOCHROMIS*** nov.

TYPE SPECIES: *Haplochromis obtusidens* Trewavas, 1928. Lake Victoria.

ETYMOLOGY. From the Greek *mylakris,* a millstone, + *chromis,* referring to the enlarged pharyngeal jaws and dentition.

DIAGNOSIS. *Gaurochromis* in which *the lower pharyngeal bone is enlarged and stout, with at least the two median tooth rows composed of enlarged and molariform teeth;* often with many additional teeth enlarged and molariform or submolariform, and others coarse and somewhat enlarged but still cuspidate.

The neurocranial apophysis for the upper pharyngeal bones has an expanded articular surface (both the parasphenoid and the basioccipital facets contributing to this enlargement), and strengthened, bullate lateral walls (especially the prootic component).

Contained species
Gaurochromis (*Mylacochromis*) *obtusidens* (Trewavas), 1928. Lake Victoria; see Greenwood (1960 : 266–9).

Research in progress at the University of Leiden, Netherlands, indicates that there is probably a second species of *Mylacochromis* in Lake Victoria (Dr C. D. N. Barel, *pers. comm.* and personal observations).

DISCUSSION

In its overall level of anatomical differentiation (except for its larger adult size), *Gaurochromis* departs but slightly from the generalized condition seen in *Astatotilapia* species. Even in its oral dentition (p. 33) *Gaurochromis* has retained the basic bicuspid tooth form and the basic dental pattern. Its derived dental features involve a reduction in tooth size (the teeth becoming finer, shorter and more slender) combined with an increase in the number of outer row teeth in both jaws.

Departure from the generalized haplochromine condition is also seen in the attenuated and fine lower pharyngeal bone in members of the nominate subgenus (p. 34) and, in the opposite direction, by the still relatively attenuate but greatly enlarged pharyngeal bone and molariform teeth in the subgenus *Mylacochromis* (see above).

For these various reasons I conclude that the species here grouped under the name *Gaurochromis* represent a monophyletic lineage distinct from *Astatotilapia,* with which genus it shares only features plesiomorphic for the Victoria–Edward–Kivu haplochromines in general.

When compared with the pharyngeal mill in *Labrochromis* (p. 40 and Fig. 21), that of *Gaurochromis* (*Mylacochromis*) species is less robust (particularly so in the undescribed taxon). This difference is apparent in specimens of all sizes, but it is more especially obvious in larger individuals.

Enlargement of the pharyngeal bones and dentition in *Gaurochromis* (*M.*) *obtusidens* prompted an earlier suggestion (Greenwood, 1960 : 265 & 268) of a possible relationship between this species and the genus *Labrochromis* (then known only from two species, *Haplochromis ishmaeli* and *H. pharyngomylus*). In turn, the resemblance between *Gaurochromis* (*M.*) *obtusidens* and *Gaurochromis* (*G.*) *empodisma* was thought to indicate a direct phyletic linkage between *Labrochromis* and the generalized *Astatotilapia* species of the Lake Victoria flock (Greenwood, 1960 : 265 & 268).

Later studies (Greenwood, 1974; and p. 42 below), indicated, however, that *Gaurochromis* (*G.*) *empodisma* and *G.* (*M.*) *obtusidens* belong to a distinct lineage and were unlikely to be linked with *'Haplochromis' ishmaeli* and *'H.' pharyngomylus* through recent common ancestry. This conclusion is apparently corroborated by the peculiar dental features of *Gaurochromis* species belonging to both subdivisions of the genus (see p. 33 above).

These features (and the form of the lower pharyngeal bone in *Gaurochromis* (*Gaurochromis*) species) also negate the idea that '*Haplochromis*' *erythrocephalus* (see p. 46) has a recent shared common ancestry with *Gaurochromis* (*G.*) *empodisma,* and also that '*Haplochromis' acidens* could be included, as a sister group, in the same major lineage (see Greenwood, 1974 : fig. 70). Incidentally, '*Haplochromis' erythrocephalus* is the '. . . small undescribed species' that was considered to be the nearest living relative of *G.* (*G.*) *empodisma* when that taxon was first described (Greenwood, 1960 : 265).

To summarize, *Gaurochromis* appears to be an independent lineage whose sister-group relationships cannot yet be determined. Its once supposed relationships with *Labrochromis* are no longer supported because the shared specialization, an enlarged pharyngeal mill, is more parsimoniously explained as the result of convergent evolution.

Within the nominate subgenus *Gaurochromis, G.* (*G.*) *angustifrons,* from Lakes Edward and George, has the most derived pharyngeal bone morphology (see Greenwood, 1973 : fig. 19) and also differs from its congeners, probably in an apomorphic way, in having a marked sexual dimorphism in adult size range, males being much smaller than females (Greenwood, 1973 : 182).

LABROCHROMIS Regan, 1920

TYPE SPECIES: *Haplochromis ishmaeli* Blgr., 1906 (not *Tilapia pallida* Blgr., 1911, as cited by Regan 1920, p. 45, footnote). Lake Victoria.

Regan (1920) apparently defined *Labrochromis* on the basis of a single specimen (BMNH 1911.3.3 : 132), a skeleton prepared from one of the paratypical series of *Tilapia pallida* Blgr., 1911. This specimen and one other paratype were misidentified by Boulenger (see Greenwood, 1960 : 275); both are clearly referrable to *Haplochromis ishmaeli* Blgr., 1906, a fact implicitly recognized by Regan in 1922. In that paper Regan remarks apropos of *H. ishmaeli,* '. . . The remarkable pharyngeal dentition might well be held to justify the genus *Labrochromis* (Regan, 1920) were it not that in all other characters the species is nearly identical with *H. cinereus'* (Regan, 1922 : 170).

Amongst the species synonymized with *H. ishmaeli,* Regan (1922 : 169) includes '. . . *Tilapia pallida* (part) Blgr., Cat. Afr. Fish. **3** : 231', but does not state specifically whether the skeletal preparation in question was included in that 'part'. However, judging from Regan's (1922) comments on *Labrochromis* quoted above, it seems reasonable to conclude that the skeleton was indeed included in the '*pallida*' material reidentified as '*ishmaeli*'.

The holotype of Boulenger's *Tilapia pallida* represents a quite distinct taxon (see Greenwood, 1960 : 233–6; and p. 43 below), one showing none of the diagnostic features for *Labrochromis* mentioned by Regan, nor any of those to be considered below.

DIAGNOSIS. Haplochromines characterized by *a massive hypertrophy of the pharyngeal mill (especially the lower pharyngeal bone and its dentition),* and having stout but generalized jaw teeth.

The lower pharyngeal bone is massive, relatively short and broad, the dentigerous surface *concave, and the articular horns short and stout. Its dentition is composed almost entirely of stout molariform teeth;* a few smaller submolariform or cuspidate teeth sometimes occur in the posterolateral angles of the dentigerous field, or as the teeth forming the perimeter of that field.

The neurocranium is of the generalized type but has a somewhat more decurved preorbital profile and a relatively higher supraoccipital crest whose outline is nearer pyramidical than wedge-shaped. *The apophysis for the upper pharyngeal bones is enlarged and stout, its expansive articular surface almost square in outline.* As compared with the generalized type of apophysis, the basioccipital facets make a much larger contribution to the articular area, and the walls of the apophysis (particularly the prootic part) are manifestly strengthened.

Outer jaw teeth, as compared with those in *Gaurochromis*, are coarser and less numerous (30–70, modal range 36–50, in the premaxilla).

Differences in the morphology and number of the jaw teeth, and the presence of a broader, more massive and more extensively molarized pharyngeal mill, are the features most readily distinguishing *Labrochromis* from *Gaurochromis.*

Description

Habitus (Fig. 22). In their overall appearance, members of the genus *Labrochromis* have a typically generalized facies, but most species do have a rather 'heavy headed' appearance.

Maximum adult size ranges from 90–140 mm SL.

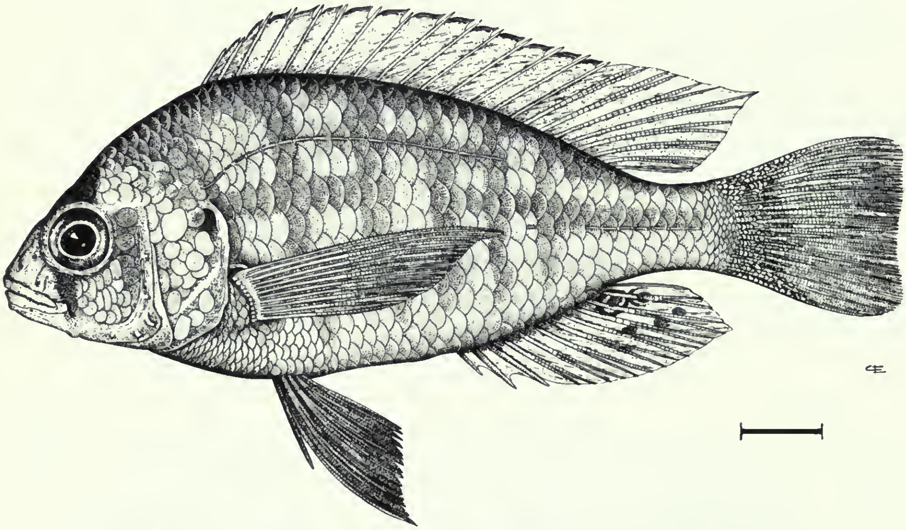

Fig. 22 *Labrochromis teegelaari.* Lake Victoria. Scale = 1 cm.

Neurocranium. The skull departs slightly from the generalized *Astatotilapia* type in having the preorbital profile gently curved (rather than straight), and the supraoccipital crest relatively high and near-pyramidical rather than wedge-shaped in profile. However, in one species (*L. ptistes*), the skull is more like the generalized kind in these features (see Greenwood & Barel, 1978 : fig. 20).

All *Labrochromis* have a stout and well-developed ventral articular apophysis for the upper pharyngeal bones, which exhibits relatively little interspecific variation in its form. Particularly noticeable are the expanded articular surface (almost square in outline), the enlarged parasphenoidal and basioccipital facets (Fig. 23), and the strengthened, somewhat bullate lateral walls (especially that part contributed by the prootics).

As the individual grows so the apophysis becomes relatively more massive. However, even in the smallest specimens examined, the basioccipital facets are larger, and the total area of the apophysis greater than in a similar-sized specimen from any other lineage (including

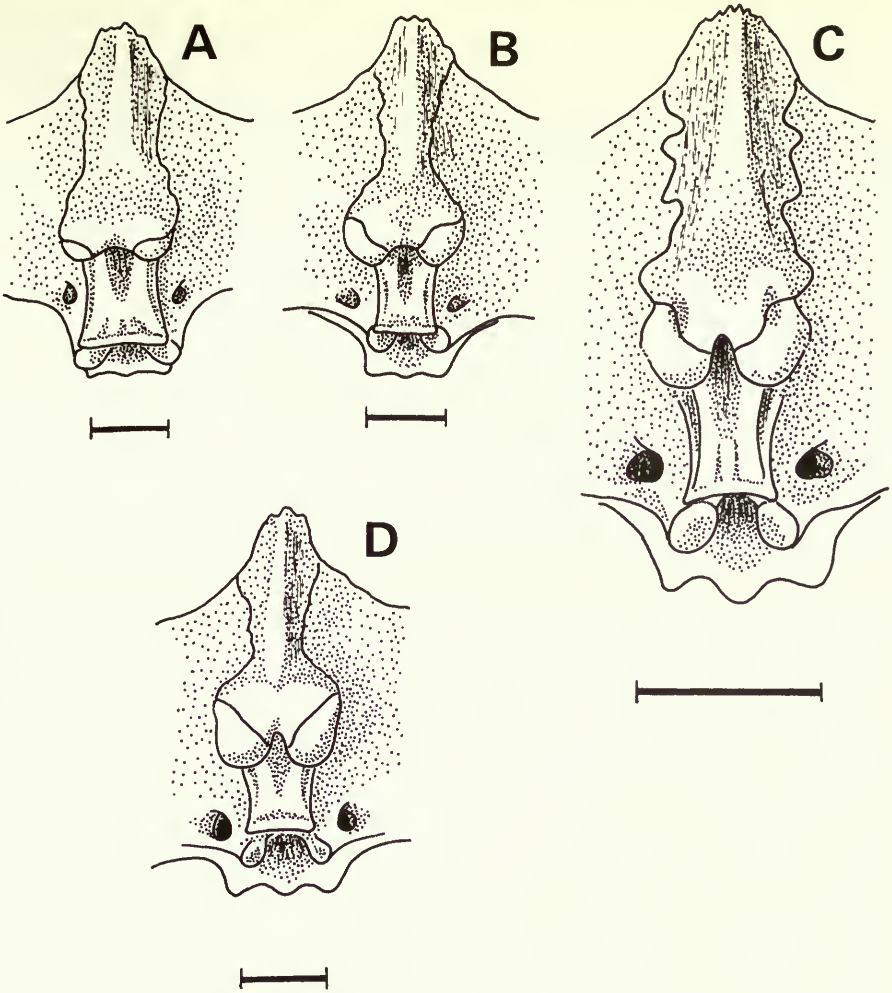

Fig. 23 Structure of the neurocranial apophysis for the upper pharyngeal bones (the pharyngeal apophysis) in various genera. A. *Gaurochromis (G.) empodisma* (typical of condition found in most haplochromine species). B. *Gaurochromis (M.) obtusidens* (see p. 36). C. *Labrochromis humilior* (the *Labrochromis* species with the least hypertrophied pharyngeal jaws in that lineage). D. *Labrochromis ishmaeli* (massive pharyngeal jaws and dentition). Scale = 3 mm.

Gaurochromis [p. 36 above], but excluding *Astatoreochromis,* see Greenwood, 1979*b* : 285–6 and also 1959*a* : 165–176; 1974 : fig. 44). This ontogenetic change in the apophysis is correlated with the size-related hypertrophy of the upper and lower pharyngeal bones and dentition.

Closest approximation to the *Labrochromis* apophyseal type is found in one species of the subgenus *Gaurochromis (Mylacochromis),* see above, p. 36, but the differences, even if less well-marked, are nevertheless apparent.

Dentition. Teeth in the outer row of both jaws are mostly of the basic bicuspid type, moderately stout to stout, slightly recurved, the neck subcylindrical, and the crown not markedly compressed. The minor cusp is small and the major one equilateral in outline. Some unicuspid teeth (otherwise similar in their morphology to the bicuspids) occur in specimens of all species at a length of *ca* 70–80 mm, the proportion increasing with the fish's length. However, even in fishes >100 mm SL, an exclusively unicuspid jaw dentition is uncommon.

There are 30–70 teeth in the outer premaxillary row, but the modal range is *ca* 36–50. Although the range overlaps that for *Gaurochromis* (44–82, see p. 33), the modal numbers in *Labrochromis* are lower (36–50 cf. 60–70). Outer jaw teeth in the latter genus are also stouter, stockier and less compressed than in *Gaurochromis,* and thus are more akin to the generalized tooth form.

Teeth forming the inner rows are small, tricuspid, and are arranged in from 1–3 (rarely 4) rows anteriorly and anterolaterally in both jaws.

Mouth. The mouth is horizontal or very slightly oblique, the lips not thickened, and the jaws equal anteriorly except in *L. humilior* where the lower jaw is usually a little shorter than the upper.

Upper jaw. As compared with the maxilla in *Gaurochromis,* that in *Labrochromis* is shorter and deeper, but its articular head has about the same degree of medial curvature (see p. 33).

The relative height of the ascending premaxillary processes ranges from shorter than the dentigerous arms of the premaxilla to as long as or slightly larger than those arms. The dentigerous arms are compressed, and anteriorly the bone is not produced into a beak or shelf.

Lower jaw. The dentary is slender and shallow, with almost the posterior half (sometimes a little less) of its alveolar surface produced into a slight lateral shelf; anteriorly there is no shelf-like projection because the body of the ramus merges gradually with the alveolar surface.

The anguloarticular complex is of the generalized type (see p. 6).

The length of the lower jaw is from 34–44% head length (modal range 37–40%), that is, within the generalized range and, at least modally, shorter than in *Gaurochromis.*

Lower pharyngeal bone and teeth (Fig. 24). In all *Labrochromis* species the lower pharyngeal bone is massive and strong, the extensive hyperossification imparting to the ventral surface a characteristic bulbous appearance (see Fig. 24C). Its articular horns are short and stout, and the posterior margin of the bone lying between them is always strongly convex, save for a slight median depression (Fig. 24C).

Because the degree of lower pharyngeal hypertrophy is positively correlated with the fish's size, 'typical' *Labrochromis* bone-form is best seen in specimens over 80 mm SL. But, even in the one species reaching only a small maximum adult size (*L. humilior, ca* 90 mm SL), the lower pharyngeal is seen to be much hypertrophied when compared with the bone from similar-sized specimens in other lineages (including *Gaurochromis* (*M.*) *obtusidens*; see p. 34). It also shows the characteristic bulbous ventral profile, and the short, stout articular horns characteristic of larger specimens (see Greenwood, 1960 : fig. 11; and 1974 : fig. 5C).

In some *Labrochromis* species the broadly triangular dentigerous surface is barely concave but in others it is markedly so, with a deep and extensive central pit (see Greenwood & Barel, 1978 : figs 26 & 30). The outline of the toothed surface is, relatively speaking, wider overall than in *Gaurochromis* (*Mylacochromis*) and, when viewed occlusally, it narrows gradually rather than rapidly from its maximum posterior width to the narrow anterior angle (Fig. 21). Generally the toothed area is as long as it is broad, but sometimes it is broader than long. In a few species, the surface, after beginning to narrow, actually broadens slightly at a point about two-thirds of the way along its antero-posterior length before it narrows again near the base of the short and deep anterior keel (see Greenwood & Barel, 1978 : figs 21 & 30).

Two outstanding features of the lower pharyngeal dentition in all *Labrochromis* species are the large size of the molariform teeth and, except in *L. humilior,* the extent to which pharyngeal molarization has proceeded. (These latter remarks, of course, are based on larger individuals; molarization is less pronounced in fishes <60 mm SL).

Apart from a few compressed and bi- or unicuspid teeth situated in the posterolateral angles of the dental field, and the teeth comprising the perimeter series (*ie* the outermost one or two teeth in each transverse row), all the remaining teeth are molariform. Teeth within the central area are the most enlarged, and rarely show any trace of the low cusp that usually is

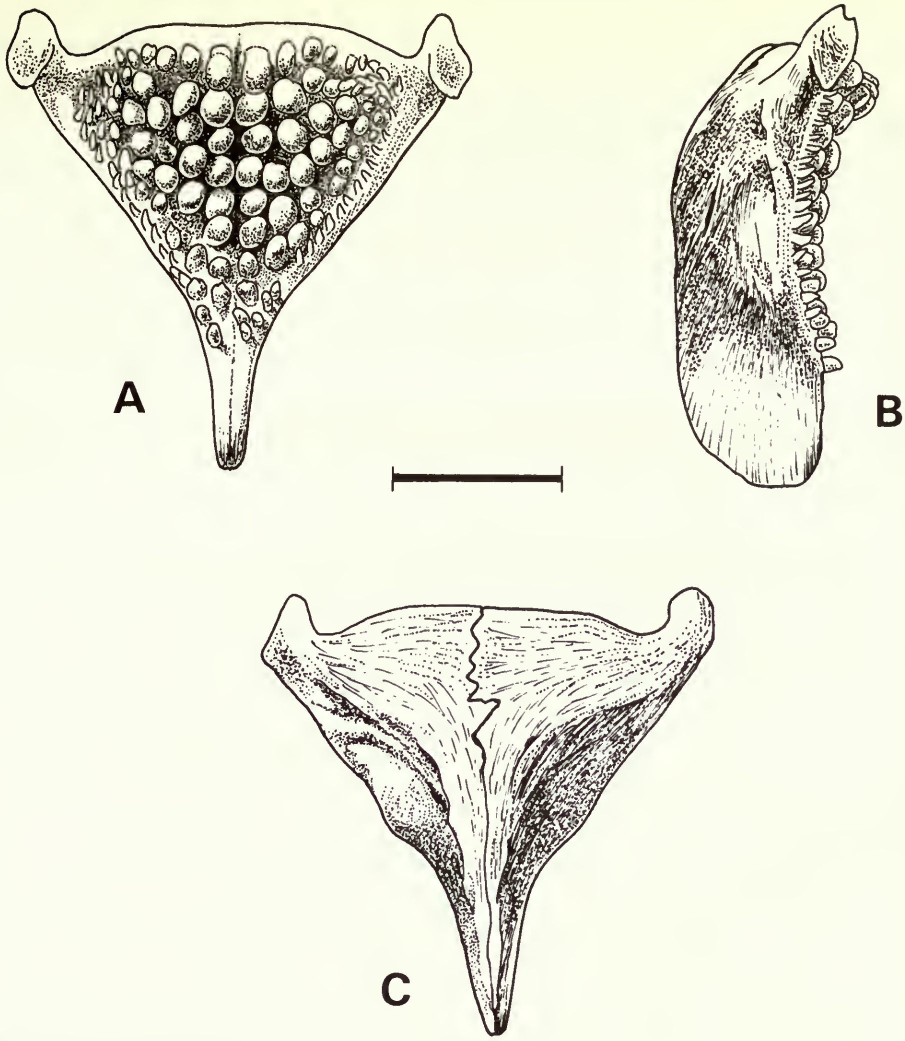

Fig. 24 Lower pharyngeal bone of *Labrochromis ishmaeli* in: A. Occlusal, B. Right lateral. C. Ventral view. Scale = 3 mm.

present on smaller molariform teeth. Loss of this cusp is at least partly attributable to wear, but even in newly erupted teeth it is insignificant.

Labrochromis humilior has proportionately fewer enlarged and molariform teeth, and these are restricted to the median rows. But, it must be stressed, these teeth are greatly enlarged, particularly when compared with the coarser teeth occurring in the median rows of the bone in other lineages (including comparable-sized specimens of *Gaurochromis* (*Mylacochromis*) *obtusidens*).

Specimens of *Labrochromis humilior* reach a maximum adult size of only *ca* 90 mm SL. When compared with like-sized individuals from other *Labrochromis* species the pharyngeal dentition is virtually identical (as is the degree to which the lower pharyngeal bone is hypertrophied). It is for these reasons (and because of its oral dentition) that I have included '*humilior*' in *Labrochromis* and not *Gaurochromis.*

All *Labrochromis* species have a correlated hypertrophy and molarization of the upper and lower pharyngeal elements.

Contained species
The taxa are grouped approximately in the order of their increasing pharyngeal mill hypertrophy and molarization.

Labrochromis humilior (Blgr.), 1911. Lake Victoria and the Victoria Nile; see Greenwood (1960 : 248–52).

Labrochromis ptistes (Greenwood & Barel), 1978. Lake Victoria; see Greenwood & Barel (1978 : 164–9).

Labrochromis mylodon (Greenwood), 1973. Lakes Edward and George; see Greenwood (1973 : 172–7).
Labrochromis ishmaeli (Blgr.), 1906. Lake Victoria; see Greenwood (1960 : 275–9).
Labrochromis pharyngomylus (Regan), 1929. Lake Victoria; see Greenwood (1960 : 270–5).
Labrochromis teegelaari (Greenwood & Barel), 1978. Lake Victoria; see Greenwood & Barel (1978 : 169–74).

Labrochromis mylergates (Greenwood & Barel), 1978. Lake Victoria; see Greenwood & Barel (1978 : 174–9).

Incertae sedis
Tilapia adolphifrederici Blgr., 1914. Lake Kivu.

I have been unable to examine the holotype of this species, a specimen once housed in the Berlin Museum but which may have been lost during the 1939–45 war. In his original description, Boulenger (1914) makes no reference to the lower pharyngeal bone of this fish, and it has not been mentioned in any subsequent redescription of the taxon (see Regan, 1921 : 637; Poll & David, 1937 : 259; Poll, 1939 : 9).

In the three BM(NH) specimens (one a skeleton), reg. nos: 1935.8.26 : 18–20, the pharyngeal mill is hypertrophied and the lower pharyngeal dentition is molarized (to an extent equaling that in *Gaurochromis* (*Mylacochromis*) *obtusidens* specimens of a comparable size). The morphology of the oral teeth, the number of outer teeth in both jaws, the shape of the dentary, and the proportions of the toothed surface on the lower pharyngeal bone are, however, of the *Labrochromis* and not the *Gaurochromis* types.

Judging from various published comments on this taxon (especially those of Regan, 1921; and Poll & David, 1937), it seems likely that at least two taxa have been confused under one name. Until more material, and the holotype, have been examined in detail, it seems inadvisable to place *Tilapia adolphifrederici* formally in *Labrochromis*. Nevertheless, the three BM(NH) specimens noted here can be referred to that genus.

Haplochromis placodus Poll, 1939, from the river Molindi, near Lake Kibuga, Zaire (Lake Edward drainage basin).

This species is known only from the holotype, and thus little detailed information is available on its anatomy. Considering the greatly enlarged and extensively molarized lower pharyngeal bone, and the nature of the oral dentition, the species probably should be included in *Labrochromis* (see also Greenwood, 1973 : 176).

Discussion

Apart from the hypertrophied pharyngeal mill (and correlated modifications to the pharyngeal apophysis on the skull base) members of this lineage share no other derived features indicative of their monophyletic origin. Some doubt can even be cast in this instance on the hypertrophied pharyngeal mill being a true synapomorphy.

An enlarged lower pharyngeal bone, coupled with some degree of dental molarization, occurs in other lineages amongst the Victoria–Edward–Kivu haplochromines, and amongst haplochromine lineages from other areas as well. *Gaurochromis* (*Mylacochromis*) *obtusidens* is an example from the Victoria area, whilst *Astatoreochromis* species furnish examples from that region and beyond. Within the polyspecific lineage *Thoracochromis*, *Th. pharyngalis* and *Th. mahagiensis* are examples from Lakes Edward and Albert, whilst species of the *Serranochromis* subgenus *Sargochromis,* together with the monotypic *Pharyngochromis darlingi,* are examples from the more southerly parts of Africa (see Greenwood, 1979).

Because these lineages do not appear to be more closely related to one another (or to *Labrochromis*) than they are to any other lineage, and since in some cases (eg in *Thoracochromis*) the species with hypertrophied mills are related to others without that specialization, the evolution of this character must have occurred independently on a number of occasions.

Thus, in the absence of unifying synapomorphies uniquely shared by all *Labrochromis* species, one cannot consider the presence of an hypertrophied pharyngeal mill (and various correlated characters) as unequivocal indicators of monophyly for the genus.

Labrochromis (in particular the species *ishmaeli* and *pharyngomylus*), has, in the past, been considered a derived relative of *Gaurochromis* (*M.*) *obtusidens* (see Greenwood, 1954 : 412–13; in that discussion, for *H. michaeli* read *H. empodisma,* see Greenwood, 1960 : 262, 266 & 269).

Later (Greenwood, 1974 : 72–4), it was suggested that *Labrochromis* (as represented by *ishmaeli* and *pharyngomylus*) and *Gaurochromis* (represented by *empodisma* and *obtusidens*) probably belonged to separate lineages. This suggestion is apparently borne out by the dental and pharyngeal differences discussed above (p. 40), differences which are apomorphic features serving to distinguish all *Gaurochromis* from every *Labrochromis* species. This general situation would still hold even if *Labrochromis* proves to be a non-monophyletic assemblage (see above).

Amongst *Labrochromis* species, *L. humilior* (Lake Victoria), with its small adult size and moderate degree of pharyngeal development, seems to be the least derived taxon. *Labrochromis ptistes, L. ishmaeli, L. pharyngomylus, L. teegelaari* (all from Lake Victoria) and *L. mylodon* (Lakes Edward and George) are at approximately the same level of anatomical derivation, whilst *L. mylergates* (Lake Victoria) appears to be the most derived species in the genus (see Greenwood & Barel, 1978 : 176–7).

In a previous analysis of the Lake Victoria flock (Greenwood, 1974 : fig. 70), *Haplochromis pallidus* (now *Astatotilapia pallida,* p. 9) was considered to be the plesiomorph sister taxon of three species now included in *Labrochromis.* This supposed relationship was based on *pallida* having somewhat enlarged median teeth on its slightly enlarged lower pharyngeal bone, and on the overall dental and syncranial similarities shared with the other species. It is apparent that the latter features are symplesiomorphies (and thus of no value as phyletic indicators), and that the pharyngeal characters are of equivocal significance. Several species have pharyngeal features like those of *A. pallida,* but in none (including *A. pallida*) is the bone so hypertrophied, nor its teeth so extensively molarized as in *Labrochromis humilior,* the least derived member of that genus. In other words, there are no clear-cut synapomorphies allowing one to postulate a recently shared common ancestry between *Astatotilapia pallida* and *Labrochromis*; at best the available evidence is but faintly suggestive of such a relationship.

ENTEROCHROMIS gen. nov.

TYPE SPECIES: *Haplochromis erythrocephalus* Greenwood & Gee, 1969. Lake Victoria.

ETYMOLOGY. From the Greek *enteron,* the bowel, + *chromis*, referring to the long intestine in members of this lineage.

DIAGNOSIS. Small haplochromines (maximum adult size range 68–88 mm SL), with a generalized body form, head shape and syncranial skeleton, but *with a long, much coiled intestine that is at least 3 or 4 times longer than the standard length.*

From other haplochromines with a long intestine, *Enterochromis* is distinguished as follows:

From *Xystichromis* (p. 46), by its narrow bands of inner jaw teeth (1–3 rows) separated from the outer row by a distinct interspace, the crowns of the outer teeth distinctly broader than the neck of the tooth, and by having *the anterior opening to the nasal lateral line canal as large as the nostril.*

From *Neochromis* (p. 49) by its straight and sloping dorsal head profile (compared with a strongly decurved one), its narrow bands of inner teeth separated from the outer series by a distinct interspace, by its unequally bicuspid, and not equally or subequally bicuspid teeth, by its elongate and not foreshortened and laterally bullate dentary, its compressed and not inflated premaxillary dentigerous arms, by its gently sloping and not near-vertically aligned ethmovomerine skull region, and by having the opening to the nasal lateral line tubule as large as or larger than the nostril.

From *Haplochromis* (Greenwood, 1979 : 278–81), by not having the major cusp in the outer teeth drawn-out, compressed, expanded, and disproportionately larger than the minor cusp. It also differs in having no elements of the inner tooth rows similar in size or cusp form to teeth in the outer series, and in its nasal opening as large as, or larger than the nostril.

DESCRIPTION

Habitus and anatomy (Fig. 25). In most respects *Enterochromis* closely resembles *Astatotilapia,* and only those features distinguishing the two taxa (or which are developed to a different degree in *Enterochromis*) will be noted.

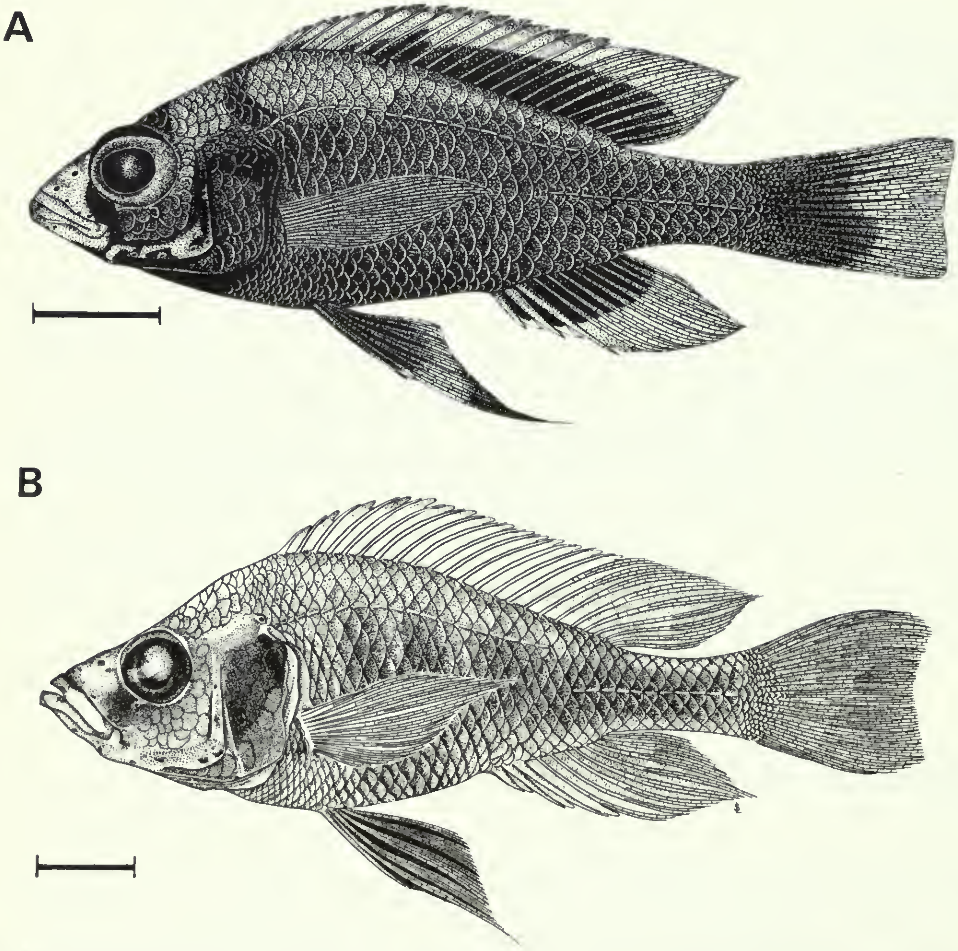

Fig. 25 A. *Enterochromis nigripinnis.* Lake George. B. *Enterochromis erythrocephalus.* Lake Victoria. Scale = 1 cm.

Neurocranium. One species (*E. erythrocephalus*) has a low preorbital skull depth (*ca* 24% neurocranial length), and the skull is narrow (otic width 50–51% neurocranial length); in the other three taxa these particular measurements are modal for the generalized skull type. (It should be noted that the skull is also narrow [*ca* 50% neurocranial width] in the otherwise generalized skull of some *Astatotilapia* species, but none has such a shallow preorbital depth as has *E. erythrocephalus.*)

Dentition. Compared with the modal condition in *Astatotilapia,* the teeth in *E. erythrocephalus* and *E. nigripinnis* are somewhat finer. Teeth in the other *Enterochromis* species, however, are of the typical *Astatotilapia* type. One or more outer teeth posteriorly in the premaxilla are enlarged and, generally, unicuspid, as they are in most *Astatotilapia* species. Also, as in that genus, some of the posterior outer teeth in both the premaxilla and the dentary are tricuspid.

No unicuspid teeth have been recorded from an anterior or anterolateral position in either jaw; possibly this is a consequence of the small adult size reached by members of the various species (see Greenwood, 1974 : 106).

There are 40–74 (modal range 50–56) teeth in the outer premaxillary row; the modal range for *Enterochromis* lies in the upper half of that for *Astatotilapia,* and the upper extremes of the *Enterochromis* range are rarely encountered in that genus.

Jaws. One *Enterochromis* species (*E. erythrocephalus*) has an oblique mouth, sloping upwards at an angle of 30°–35° (occasionally 40°) to the horizontal; the mouth in the remaining species is almost horizontally aligned.

Cephalic lateral line pores. All *Enterochromis* species, as far as I can determine, are outstanding amongst at least the Victoria–Edward–Kivu haplochromines in having the anterior opening to the nasal lateral line tubule as large (or almost as large) as the nostril. In other lineages the canal opening is much smaller.

Gut. The intestine in *Enterochromis* is long (*ca* 3–4 times the standard length) and much coiled. The folding is mostly in a horizontal plane, with 3 or 4 coils arranged below the elongate, greatly distensible stomach; posteriorly the intestine appears to be thrown into at least one vertical loop.

Lower pharyngeal bone and dentition (see also Greenwood & Gee, 1969 : 12–13, 21; and Greenwood, 1973 : 157). The bone is slender, with a triangular and equilateral dentigerous surface. Except for one species, all the teeth are fine, strongly compressed and of approximately the same size; even the posterior transverse row is made up of teeth only a little stouter than the others. In the exceptional species (*E. cinctus*), the teeth are somewhat coarser, and those in the two median rows are slightly stouter than the others. But, even in *E. cinctus* all the pharyngeal teeth are relatively finer and more compressed than those in any *Astatotilapia* species.

Again with the exception of *E. cinctus,* the teeth are numerous and close set, producing a coarse dental felt (coarse that is, compared with the dental felt in most tilapiine species of the genera *Tilapia* and *Sarotherodon,* but fine in comparison with the majority of haplochromine species).

In *E. cinctus* the teeth are more widely spaced and the dental felt is, as a result, coarser.

Contained species

The taxa are listed in approximately the order of their increasing derivation from the generalized condition.

Enterochromis cinctus (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 15–19).

Enterochromis paropius (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 10–15).

Enterochromis nigripinnis (Regan), 1921. Lakes Edward and George; see Greenwood (1973 : 151–9).

Enterochromis erythrocephalus (Greenwood & Gee), 1969. Lake Victoria; see Greenwood & Gee (1969 : 19–24).

DISCUSSION

The long, much coiled intestine of *Enterochromis* may indicate a somewhat distant common ancestry with the other phytophagous genera, namely, *Haplochromis, Xystichromis* and *Neochromis.* This question is discussed on p. 48.

Earlier attempts to relate *E. erythrocephalus* with the *Gaurochromis* lineage, in particular with *G.* (*G.*) *empodisma* (see Greenwood, 1974 : 66–7 and fig. 70; also Greenwood & Gee, 1969 : 23) can no longer be substantiated. The two taxa share no unequivocally derived features, and each has its own apomorph features which suggest relationships with other lineages (see p. 37).

Within the genus, *E. erythrocephalus* is the most derived species. Its narrow and preorbitally shallow skull, the fine and densely toothed lower pharyngeal bone, and the oblique mouth, are all characters contributing to that status, as are the high number (12) and fine shape of the gill-rakers (see Greenwood & Gee, 1969 : 20). Otherwise, little else can be said about intragroup relationships.

XYSTICHROMIS gen. nov.

TYPE SPECIES: *Chromis nuchisquamulatus* Hilgend., 1888. Lake Victoria; see Greenwood (1956*b* : 241).

ETYMOLOGY. From the Greek '*xyster*', one who scrapes, + *chromis,* alluding to the grazing habits of its member species.

DIAGNOSIS. Small haplochromines with a maximum adult size range of 85–105 mm SL, *a much coiled and long intestine* (*ca* 3–4 times SL), and the *broad bands (4–6 rows deep) of inner teeth anteriorly and anterolaterally in both jaws, narrowly, if at all separated from the outer tooth row.*

Neurocranium of the generalized type except that the *preorbital skull profile slopes more steeply and the supraoccipital crest is deeper and more pyramidical in shape.*

Teeth in the outer row of each jaw very close set (usually contiguous), moveably implanted, tall, and slender but strong, showing only a slight antero–posterior decline in their height and size. All (except for a few unicuspids posteriorly in the upper jaw) are unequally bicuspid, the minor cusp prominent but clearly smaller than the major one; the crown is not distinctly broader than the neck.

Inner row teeth are tricuspid, those of the outermost one or two rows almost as large as their counterparts in the outer row.

Lower pharyngeal bone without molariform or submolariform teeth; in some specimens the teeth of the median rows are enlarged and coarser than those of the lateral rows.

From other genera with long and coiled intestines, *Xystichromis* is distinguished as follows:

From *Neochromis,* by its gently sloping, not strongly decurved dorsal head profile, its unequally as opposed to equally or subequally bicuspid teeth, its elongate and not foreshortened dentary (which also is not bullate laterally), and by the ethmovomerine region of the skull sloping at an angle of 40°–50° to the horizontal and not almost vertically aligned.

From *Haplochromis,* particularly by its unequally bicuspid teeth, as compared with the very unequally bicuspid teeth in which the major cusp is protracted and compressed, and the minor cusp is virtually or entirely suppressed.

From *Enterochromis* it is distinguished by the characters listed on p. 43.

DESCRIPTION

Habitus (Fig. 26). There is little to differentiate members of this genus from *Astatotilapia* species. Maximum adult size range is 86–105 mm SL; no information is available on the size at which sexual maturity is reached.

Neurocranium. Skull form in *Xystichromis* is essentially like that in *Astatotilapia* except that the preorbital skull region slopes more steeply, and the supraoccipital crest is relatively deeper and more pyramidical in outline.

Dentition. It is the dentition of *Xystichromis* which provides the greatest number of derived features and, indeed, the synapomorphies uniting members of the lineage.

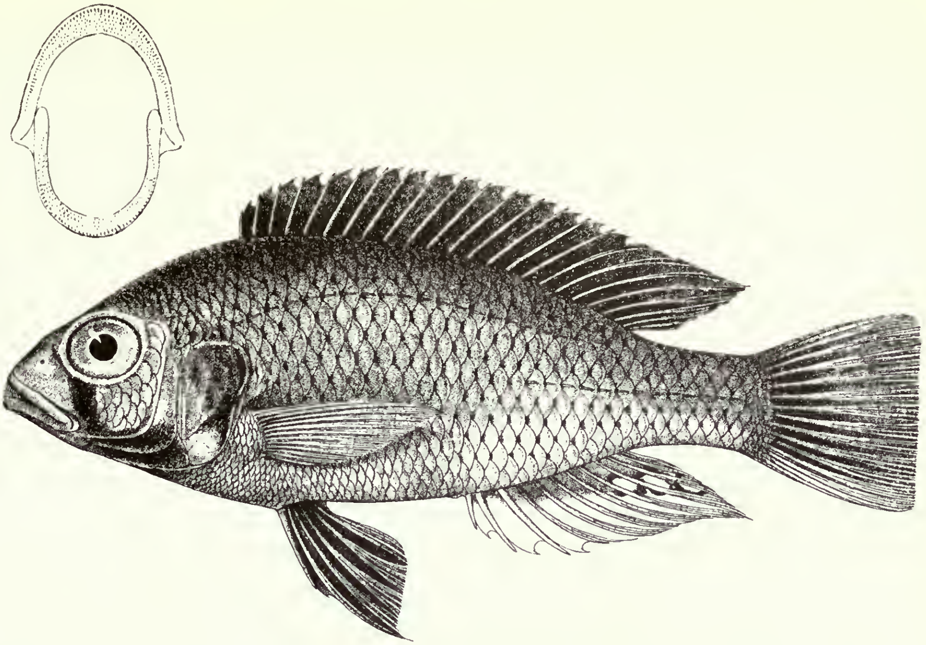

Fig. 26 *Xystichromis bayoni* Lake Victoria. About 1·3× natural size. Inset: the dental pattern of the upper and lower jaws (about 2·5× natural size).

Outer row teeth in both jaws are very close-set (contiguous or partially continguous), moveably implanted and tall, with only a slight antero-posterior decline in their height and overall size. Apart from one to three enlarged caniniform teeth posteriorly in the premaxilla, and the occasional intercalation of a tricuspid tooth posterolaterally, the teeth are all unequally bicuspids. The acutely pointed minor cusp is prominent but distinctly smaller than the major cusp, which has a somewhat obliquely slanting posterior margin and a broadly acute tip. Many teeth have this posterior margin produced into a low flange over part of its length; such flanges are known from members of other lineages as well (*eg Astatotilapia macropsoides, A. elegans* and *A. aeneocolor,* from Lake George (Greenwood, 1973), and *Gaurochromis empodisma* in Lake Victoria); their significance is not known.

Although relatively slender, the outer teeth in *Xystichromis* are robust and but slightly recurved. They also differ from the generalized bicuspid tooth in not having the crown distinctly broader than the neck and body of the tooth; as a result, the anterior and posterior margins of the entire tooth are almost parallel. The crown is also somewhat more compressed than in the generalized bicuspid tooth, although it could not be described as flattened.

There are 36–70 (modal range 50–65) teeth in the outer premaxillary series.

Because the insertion line of the outer teeth is lower than that of the inner teeth, the crowns of the teeth in both series are, effectively, at the same level. Presumably this is a feature associated with the algal-grazing habits of the known species.

Although the modal number of inner tooth rows in any one species is elevated in comparison with the generalized condition, the lower end of the total range (2–8) does overlap that for *Astatotilapia,* but *Xystichromis* individuals with only 2 or 3 inner rows are uncommon.

Upper jaw. Compared with the generalized type of premaxilla, that in *Xystichromis* has a broader alveolar surface and the dentigerous arms are slightly inflated anteriorly and anterolaterally.

Lower jaw. The dentary is not deep and foreshortened (as in *Neochromis,* see p. 51), but neither is it as slender as the dentary in *Astatotilapia.*

Lower pharyngeal bone and dentition. Both the bone and its teeth are of the generalized type. There is some intrageneric variation in the relative width of the dentigerous surface, with one species, *X. phytophagus,* having a distinctly broad and stout bone (see Greenwood, 1966 : 304–6). Some of the median teeth are coarse, and may even be enlarged posteriorly in *X. bayoni.*

Gut. The intestine in *Xystichromis* is long (at least 3 to 4 times the standard length) and much coiled; the stomach is large and greatly distensible.

Contained species

Since no intralineage relationships can be determined the species are listed alphabetically.

Xystichromis bayoni (Blgr.), 1911. Victoria Nile.

This species was given the replacement trivial name '*niloticus*' by Greenwood (1960 : 243) who, disagreeing with Regan's (1922 : 169) idea that the taxon was synonymous with *Haplochromis humilior*, resurrected it to full specific status within the genus *Haplochromis* as then defined.

At that time the name '*bayoni*' was preoccupied by *Haplochromis bayoni* (Blgr.), 1909, and so a new trivial name was required for Boulenger's (1911) '*bayoni*'. Hence the introduction of '*niloticus*' as a replacement (see Greenwood, 1960 : 243–5). Since Boulenger's 1909 '*bayoni*' is now placed in the genus *Prognathochromis* (see p. 19 above), Boulenger's 1911 name is again available for the species listed here.

Xystichromis nuchisquamulatus (Hilgend.), 1888. Lake Victoria and the Victoria Nile; see Greenwood (1956*b* : 241–3).

Xystichromis phytophagus (Greenwood), 1966. Lake Victoria; see Greenwood (1966 : 303–9).

DISCUSSION

Apart from its dental specializations and long, coiled intestine, *Xystichromis* is, anatomically speaking, a generalized haplochromine.

However, the dental pattern, the tall and slender but robust teeth, and the enlarged, broad-banded inner teeth do resemble those of *Neochromis,* a lineage with which *Xystichromis* also shares the derived feature of an elongate and much coiled gut (see p. 52).

It is possible, therefore, that these two genera share a common ancestor in which such dental and alimentary features are present, and that they should be ranked as sister taxa (but see also p. 52).

A long coiled gut is also present in *Haplochromis* and in *Enterochromis* (see p. 45) but neither genus shares all the dental synapomorphies common to *Xystichromis* and *Neochromis. Haplochromis* has a uniquely derived crown form in its outer jaw teeth (see Greenwood, 1979 : 278–9), but also has broad bands of teeth anteriorly and anterolaterally in the jaw. In that latter feature it shares an apomorph character with both *Neochromis* and *Xystichromis. Enterochromis* has an essentially plesiomorph haplochromine dentition (see p. 45).

If the shared apomorphy of a long, much coiled gut really does indicate a common ancestry for all four genera, then the various dental specializations suggest that *Xystichromis, Neochromis* and *Haplochromis* are more closely related to one another than any one is to *Enterochromis.* In other words, *Haplochromis,* because of its greater dental specializations, is the sister taxon of *Xystichromis* and *Neochromis* combined, and *Enterochromis,* because of its relatively generalized dentition is the plesiomorph sister group to all three.

An acceptance of this solution is complicated by various derived syncranial features which *Neochromis* alone shares with a number of other lineages, and which might therefore indicate its relationship to them (the dental features being then taken as parallelisms). However, the first set of relationships proposed above is the more parsimonious since its resolution involves fewer and less profound dental and anatomical changes (see discussion p. 52).

Intrageneric species grouping within *Xystichromis* is not possible on the basis of available data; no two species appear more closely related to one another than either does to the third member of the lineage.

NEOCHROMIS Regan, 1920

Type species: *Tilapia simotes* Blgr., 1911 (see Regan, 1920 : 45), now considered a junior subjective synonym of *Tilapia nigricans* Blgr., 1906 (see Greenwood, 1956*b* : 237).

Diagnosis. Small haplochromines (maximum adult size 95 mm SL), with *a very strongly decurved dorsal head profile (sloping at 70°–80° to the horizontal), a long, much coiled intestine (ca* 3–4 times SL*), broad bands of inner teeth anteriorly and anterolaterally in both jaws, not separated from the outer row, and equally or subequally bicuspid outer teeth.*

Neurocranium with a strongly decurved preorbital face, the ethmovomerine region almost vertically aligned.

Dentary markedly foreshortened, deep and stout, its anterior margin strongly curved medially so that the anterior outline of the lower jaw is almost rectangular. The region of the dentary surrounding its posterior division into coronoid and horizontal limbs is markedly bullate. Length of lower jaw 30–38% head length, modal range 34–36%.

The anguloarticular complex of the lower jaw is stout, *the anterior point of its anteroventral arm blunt or rectangular* (never acute).

Premaxilla with noticeably inflated dentigerous arms, almost cylindrical in cross section, the alveolar surfaces broad; its ascending processes as long as the dentigerous arms.

Outer jaw teeth tall, slender but robust, and without any marked antero-posterior decline in height; moveably implanted and very close set (contiguous). Cusp form characteristic, the minor (*ie* posterior) cusp well-developed and only a little smaller than the major (*ie* anterior) cusp, from which it is separated by a narrow notch; the points of each cusp are almost spatulate. The crown is compressed relative to the cylindrical neck and body of the tooth (but is not flattened), and is broader than the body.

Inner tooth rows numerous (3–8, usually 5 or 6), the teeth in a row contiguous, and the rows close set; there is no discrete interspace between the outermost row and the outer row of teeth. Inner teeth tricuspid (with all cusps of about the same height), the teeth in the two outermost rows distinctly larger than those of the innermost rows.

Teeth in the median rows on the lower pharyngeal bone relatively stout in two species, not so in the remainder.

Features distinguishing *Neochromis* from the other taxa with long, coiled, intestines are listed on p. 44 for *Enterochromis*, and p. 46 for *Xystichromis.*

Description

Habitus (Fig. 27). The strongly decurved and steep dorsal head profile, and the near-horizontal mouth, combine to give the pug-headed appearance which is so characteristic a feature of all *Neochromis* species. None reaches a large adult size (*ca* 95 mm SL).

Neurocranium. The preorbital face of the skull is very strongly decurved (sloping at an angle of *ca* 70°–80° to the horizontal), the ethmovomerine region is aligned almost vertically and its tip extends ventrally to a point below a horizontal through the anterior part of the parasphenoid (see Fig. 28). The supraoccipital crest is of variable outline and relative height, but it is always somewhat deeper and less wedge-shaped than in a generalized skull.

Dentition. Teeth in the outer row of both jaws are tall (and without any marked antero-posterior decline in height), slender but strong, are moveably implanted and so close-set as to be continguous. There are 40–70 teeth (modal range 50–56) in the outer premaxillary row.

One species (*N. nigricans*) has the last, or sometimes the last two teeth in the premaxillary row enlarged and unicuspid, but usually in that species, and in the other two *Neochromis* species, the posterior teeth are like the others.

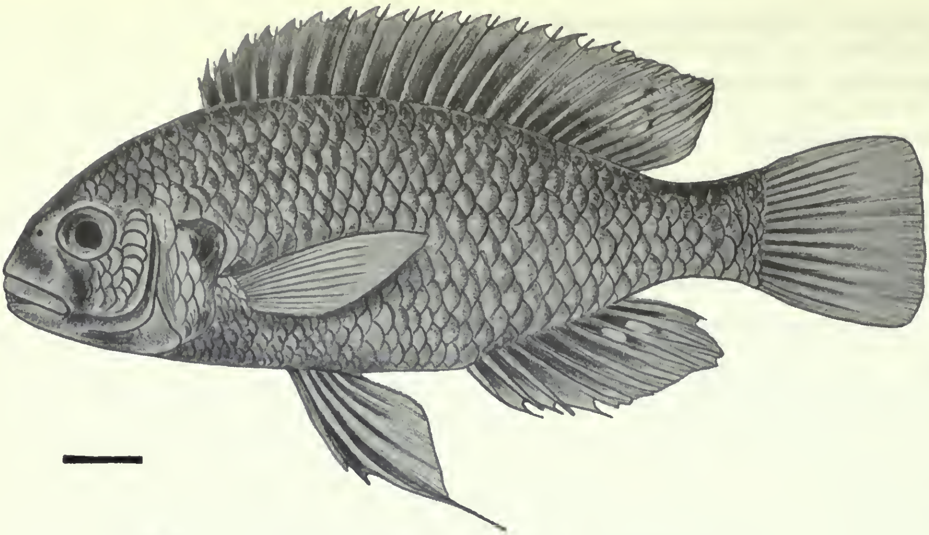

Fig. 27 *Neochromis nigricans.* Lake Victoria. Scale = 1 cm.

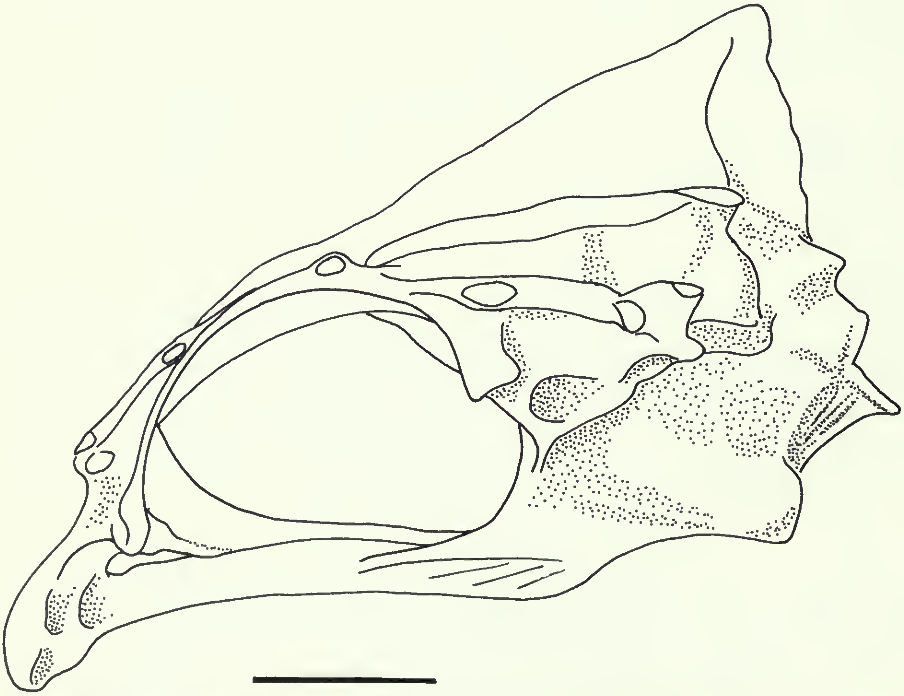

Fig. 28 Neurocranium of *Neochromis nigricans*; left lateral view. Scale = 3 mm.

Cusp form in *Neochromis* is very characteristic (Fig. 29). The inner (*ie* posterior) cusp is well-developed, often only a little smaller than the major (*ie* anterior cusp), and is directed obliquely backwards (rather than vertically upwards). The points of both cusps are spatulate or somewhat acutely spatulate (but never acute). The crown is compressed (relative to the cylindrical neck and body of the tooth) but is by no means flattened; it is also broader than the neck so that the margins of the tooth are not parallel **(cf.** *Xystichromis* p. 47**)**.

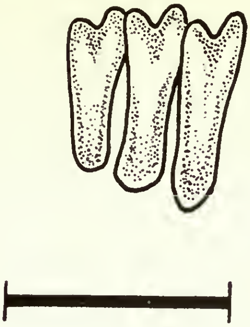

Fig. 29 Outer row teeth from the dentary of *Neochromis nigricans*, viewed labially. Scale = 1 mm.

Inner tooth rows are composed of moveably implanted tricupsid teeth in which the two lateral cusps are of almost the same height and width as the median one. Those teeth forming the two outermost rows in each jaw are enlarged, and even those in the remaining rows are relatively larger than their counterparts in other lineages except *Xystichromis*; all, however, are shorter than the outer row teeth. There are 3–8 (modes 5 or 6) rows of inner teeth anteriorly and anterolaterally in each jaw, and one or two rows laterally. Teeth in these rows are contiguous, and the rows themselves are close set so that only a very narrow interspace separates them; the interspace between the outermost row of the inner series and the outer tooth row is barely discernible. Thus, as compared with *Xystichromis*, although the area covered by the inner tooth rows is almost the same, there are more rows of teeth in *Neochromis*, and the rows are set much closer together (see p. 47). As in *Xystichromis*, tooth insertion levels are such that the crowns of the inner and outer row teeth are at the same level despite the inner teeth being slightly shorter.

Mouth. The mouth is horizontal and the jaws equal anteriorly; the lower jaw is broad and its anterior outline, when viewed from below, is almost rectangular.

Upper jaw. The premaxilla has notably inflated dentigerous arms, oval to near-circular in cross section anteriorly and anterolaterally, but somewhat more compressed posteriorly. Compared with the generalized premaxilla, that in *Neochromis* has a broader alveolar surface, and the ascending processes are longer (as long as the dentigerous arms).

Lower jaw. The dentary is deep relative to its length, and has the appearance of being a stout, foreshortened bone (Fig. 30). Anterolaterally, each ramus curves inwards rather abruptly so that the anterior margin of the entire jaw is rectangular.

The anguloarticular complex is stout, with the anterior point of its anteroventral arm blunt or rectangular in outline.

The crown of the coronoid process (the ascending arm) on the dentary has a slight but definite medial inflection.

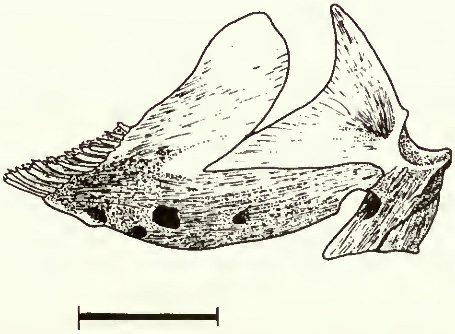

Fig. 30 Dentary of *Neochromis nigricans*, left lateral view. Scale = 3 mm.

Lower jaw length in *Neochromis* (30–38% head length, modal range 34–36%) broadly overlaps that in the majority of non-piscivore lineages with small-sized adults (*ie* < 110 mm SL), although the modal length in several of these species is higher (40–44%) than in *Neochromis.* Lower jaw width in *Neochromis* (1·0–1·4, mode 1·2 times longer than broad) also overlaps that in lineages with a generalized syncranial morphology, but modally it is distinctly greater in *Neochromis.*

Lower pharyngeal bone and dentition. The dentigerous surface is triangular and as broad as it is long. In *Neochromis nigricans* and *N. serridens* the teeth are fine and compressed bicuspids, densely arranged on the bone, with only the posterior transverse row composed of stouter teeth; *N. fuscus,* however, has all the pharyngeal teeth relatively coarser, less closely set and with the two median rows composed of somewhat enlarged (but cuspidate) teeth.

Gut. The intestine is long (at least 3–4 times longer than the standard length) and much coiled; the stomach is large and distensible.

Contained species

For the possible interrelationships of these taxa, see below.

Neochromis nigricans (Blgr.), 1906. Lake Victoria and the Victoria Nile (*Tilapia simotes* Blgr., 1911, the type species of *Neochromis,* is currently considered to be a junior synonym of this species; see Greenwood, 1956*b* : 237–40).

Neochromis serridens (Regan), 1925. Lake Edward; see Trewavas (1933 : 327–8).

Neochromis fuscus (Regan), 1925. Lake Edward; see Trewavas (1933 : 329).

DISCUSSION

In all *Neochromis* species certain derived syncranial features, such as the strongly decurved preorbital skull, the deep, foreshortened dentary, the stout anguloarticular complex, the laterally bullate dentary, and the inflation of the premaxillary arms, are shared either *in toto,* in part or in varying degrees of expression, with several lineages (*Macropleurodus, Ptyochromis, Hoplotilapia, Platytaeniodus, Paralabidochromis, Lipochromis, Schubotzia* and *Allochromis*).

It is difficult to assess the significance of this situation. Other synapomorphies occurring in these taxa, but not in *Neochromis,* point to further groupings that can be made amongst them (see discussions on pp. 92–94) and suggest that the syncranial features shared with *Neochromis* are, at most, an indication of distant (rather than recent) common ancestry. Alternatively, the syncranial synapomorphies could be parallelisms associated with the independent evolution of strong jaws and dentition (often multiseriate), or of a multiseriate dentition alone.

The latter interpretation must be invoked if the hypothesized relationship between *Neochromis, Haplochromis, Enterochromis* and *Xystichromis,* put forward on p. 48, is accepted. It should be stressed that this relationship, unlike that associating *Neochromis* with *Macropleurodus, Ptyochromis* etc, does not require the independent evolution of a long gut (and presumably associated physiological changes) in *Neochromis,* nor the unique development of its dental type within a 'lineage' having totally different dental specializations and a simple gut form.

Thus, it is more parsimonious to propose that *Neochromis* is related to the other species with long, coiled intestines and bicuspid teeth, modified though the teeth may be in some species, than to the eight other genera with which it shares some syncranial specializations (see pp 48–49).

Unfortunately there are few available specimens of *Neochromis serridens* and *N. fuscus,* the Lake Edward representatives of the genus. As a result, little is known about the range of variation in critical characters in these species, but it would seem that the dentition of *N. nigricans,* the Lake Victoria representative, is less specialized than that in the Edward species. Since *Neochromis nigricans* has teeth which are more unequally bicuspid than in the others, and its inner rows are generally fewer in number, the Edward taxa would seem to be more closely interrelated than either is to *N. nigricans.*

HAPLOCHROMIS Hilgendorf, 1888

TYPE SPECIES: *Chromis (Haplochromis) obliquidens* Hilgendorf, 1888. This now much impoverished genus is redescribed in the first part of this paper (see Greenwood, 1979 : 278–81).

Contained species
The taxa are grouped and listed in order of their increasing derivation.

Haplochromis limax Trewavas, 1933. Lakes Edward and George; see Greenwood (1973 : 167–72).

Haplochromis annectidens Trewavas, 1933. Lake Nabugabo; see Greenwood (1965 : 329–35).
Haplochromis lividus Greenwood, 1956. Lake Victoria; see Greenwood (1956*b* : 232–7).

Haplochromis astatodon (part) Regan, 1921. Lake Kivu; see Greenwood (1979 : 280).
Haplochromis obliquidens Hilgendorf, 1888. Lake Victoria; see Greenwood (1956*b* : 226–32).

PSAMMOCHROMIS gen. nov.

TYPE SPECIES: *Pelmatochromis riponianus* Blgr., 1911 (as redefined by Greenwood, 1960 : 252–6). Lake Victoria.

ETYMOLOGY. From the Greek '*psammos*', sand, + *chromis,* referring to the sandy substrata seemingly preferred by most members of the genus.

DIAGNOSIS. Haplochromines reaching a maximum adult size of 100–123 mm SL, the body relatively slender to moderately deep (31–43% SL, modal range 36–38%); lips thickened in all species, the lower lobate in one.

Neurocranium of a near-generalized type but *shallower in the otico-occipital region (40–46% neurocranial length).*

Outer jaw teeth tall and slender, their crowns recurved and either compressed or finely acuminate and cylindrical in cross-section. Very unequally bicuspid teeth present in specimens of all sizes, but unicuspids predominate in fishes >80–90 mm SL; 24–68 teeth in the outer premaxillary row.

Inner teeth tall and slender, tri- or unicuspid, and usually implanted so as to lie almost horizontally; commonly arranged in 2–4 rows anteriorly.

Premaxilla with a definite anterior beak, its ascending processes longer than the dentigerous arms, which have a slight ventral decurvature over the posterior half (more marked in some species than in others).

Dentary with a very distinctive form, each ramus noticeably inflated anteriorly and anterolaterally, this circumscribed swelling extending almost to the bone's ventral profile. Over this region (and slightly behind it) the narrow outer margin of the alveolar surface dips distinctly downward so that the outer tooth row also has a ventral inflection (see Fig. 32).

Lower pharyngeal bone in some species moderately stout, its median teeth enlarged and submolariform, but the bone slender and without enlarged teeth in others.

DESCRIPTION
Habitus (Fig. 31). There are few outstanding features in the habitus of most *Psammochromis* species. The body varies from relatively slender to moderately deep (31–43% SL, modal range 36–38%), the dorsal head profile is straight or gently curved, and slopes fairly steeply. All species have thickened lips, and the lower lip may be lobate in *P. aelocephalus*, which species also has a highly variable snout form (noticeably protracted in some individuals; see Greenwood, 1959*b* : 214–17).

Maximum adult size ranges from 100–123 mm SL; individuals reach sexual maturity at a length of 80–85 mm in those species attaining the larger maximum sizes.

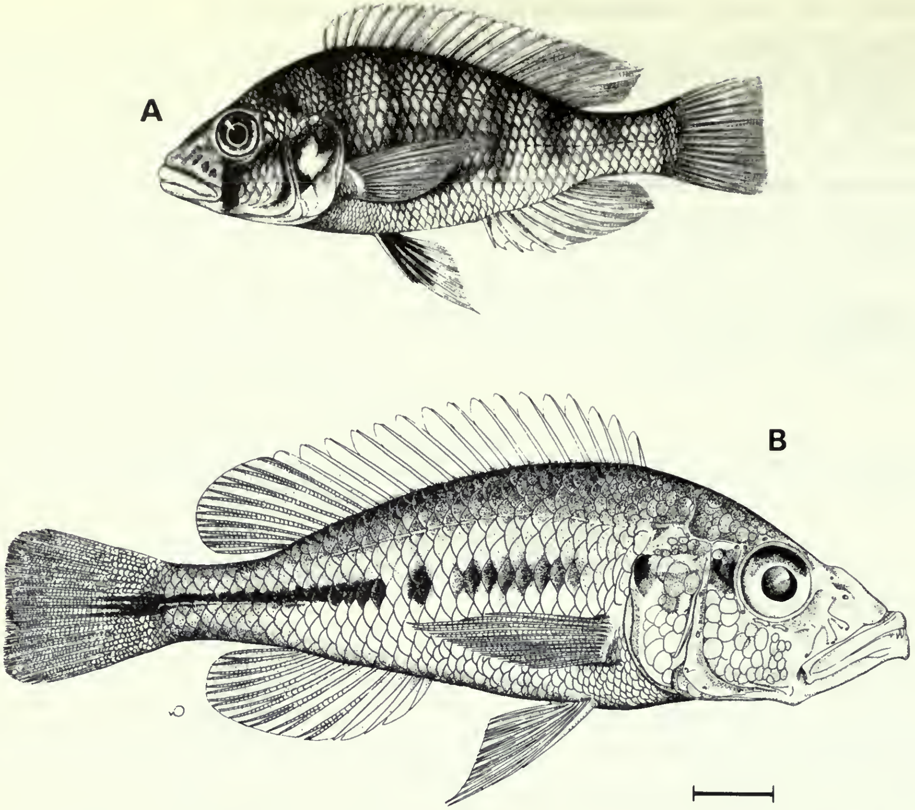

Fig. 31 A. *Psammochromis riponianus.* Lake Victoria. About two-thirds natural size. B. *Psammochromis cassius.* Lake Victoria. Scale = 1 cm.

Neurocranium. The skull is of a near-generalized type but has a lower otico-occipital region (depth 40–46% neurocranial length) so that the preotic dorsal profile slopes downwards and forwards fairly gently; the supraoccipital crest is relatively low and is wedge-shaped in profile.

Although in one species (*P. riponianus*) some individuals have the pharyngeal mill enlarged to a degree comparable with that in *Gaurochromis* (*Mylacochromis*) *obtusidens* (see p. 34), there is no corresponding enlargement of the pharyngeal apophysis on the skull base. As compared with those congeneric species not having an enlarged pharyngeal mill, the parasphenoid contribution to the apophysis in *P. riponianus* is slightly more expansive, but the basioccipital facets are barely larger.

Dentition. The outer row jaw teeth are slender and tall, the body and recurved crowns either relatively compressed (only the lower part of the tooth cylindrical in cross-section) or the crown is finely acuminate and the whole tooth cylindrical in cross-section and very slender. Species with the latter type of teeth have the teeth widely spaced, especially in the lower jaw.

When bicuspid, the coarser type of tooth has the minor cusp greatly reduced, the major cusp vertically protracted and pointed; bicuspid forms of the finely acuminate unicuspids are as yet unknown.

Some bicuspid teeth are present in most specimens of all other species, but predominate only in fishes <90 mm SL; above that size, unicuspids and, or, weakly bicuspid teeth are more frequent. *Psammochromis cassius* is unusual in having only unicuspid teeth present in specimens as small as 70 mm SL, and, apparently, in having some lower teeth lying outside, or even penetrating into, the upper lips (see Greenwood & Barel, 1978 : 162).

A characteristic feature of two species from Lake Victoria (*P. riponianus* and *P. saxicola*), is the very abraded crowns on most outer teeth, which then appear bluntly incisiform.

Inner teeth are also slender and tall, tricuspid in small individuals but unicuspid in larger fish, implanted so as to lie almost horizontally, and generally embedded deeply in the oral mucosa (Greenwood, 1960 : 254). There may be as many as 5 rows of inner teeth anteriorly in each jaw; the modal numbers are, however, 2–4.

Mouth. Lips are clearly and equally thickened, but in one species (*P. aelocephalus*) the lower lip may be produced anteriorly into a small but definite mental lobe. The mouth is horizontal or but slightly oblique; this, combined with the thickened lips and particular head profile, impart to the members of this lineage a very characteristic but indefineable physiognomy (see Fig. 31; also figs 13 & 14 in Greenwood, 1960; and figs 20 & 21 in Greenwood, 1973).

Upper jaw. The premaxilla is somewhat expanded and protracted anteriorly and antero-medially into a definite beak or peak. Its ascending processes are longer than the dentigerous arms, which have a slight but distinct ventral curvature over their posterior halves (the curve more marked in some species than in others).

The maxilla is elongate and slender in *P. saxicola* but relatively foreshortened and deep in the other species. In none is the medial face of the posterior arm strongly concave (and thus the lateral aspect is but slightly bullate), and none has a marked medial curvature of its articular head.

Lower jaw. The most trenchant and diagnostic synapomorphy linking members of this lineage lies in the morphology of the dentary (Fig. 32).

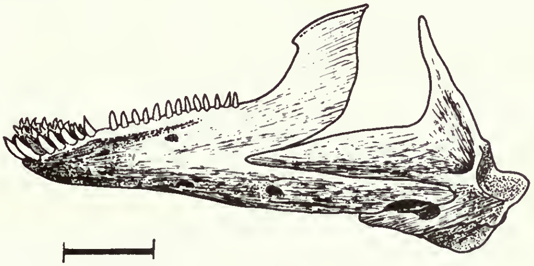

Fig. 32 Dentary of *Psammochromis saxicola* in left lateral view. Scale = 3 mm.

Anteriorly and anterolaterally the bone immediately below the alveolar surface is distinctly inflated, the well-circumscribed swelling extending almost to the ventral margin of each ramus. Over this swollen region, and a little behind it as well, the narrow outer margin of the alveolar surface dips downwards so that the line of outer teeth also dips ventrally in that region of the jaw. Consequently the tips of the outer teeth are on a level with those of the much smaller inner teeth.

The dentary also departs from the generalized type in being relatively shallower. Thus, although the length of the entire lower jaw (dentary + anguloarticular) is within the 'generalized' range (33–49% head length) it gives the impression of being much more slender and attenuated.

No mental protuberance is developed at the dentary symphysis. Indeed, the ventral symphysial profile slopes backwards so that the jaw appears 'chinless', except for a slight vertically directed ventral projection at the symphysial base.

Lower pharyngeal bone and teeth. There is considerable inter- and some intraspecific variation in the stoutness of the bone, and there are correlated differences in the nature of its dentition (see Greenwood, 1959 : 216; 1960 : 254 & 258, and figs 4 & 5).

All or some of the teeth in the four median rows may be enlarged and are often molariform or submolariform. The remaining teeth, and sometimes those of the median rows as well, are weakly cuspidate and compressed (except, as is usual, for the robust teeth in the posterior transverse row).

Squamation. Except in two species, the scales anteriorly and ventrally on the chest region are distinctly smaller than those on the ventral flanks and belly, and appear to be more deeply embedded. There is, however, no abrupt size change between the scales of the two regions, which grade imperceptibly into one another (see Greenwood, 1979 : 270–2).

In the exceptional taxa (*P. acidens* and *P. cassius*) the chest scales are not obviously smaller than the belly scales, and do not give the appearance of being deeply embedded.

Contained species

The taxa are listed in order of their increasing apomorphy.

Psammochromis graueri (Blgr.), 1914. Lake Kivu.

Amongst the BM(NH) material identified as *graueri*, only three specimens (BMNH reg. nos: 1914.4.8 : 16, 19 & 20) are apparently conspecific. The concept of *graueri* used in this paper is thus based on those specimens, of which one, reg. no. 1914.4.8 : 20, a fish 99·0 mm SL, is chosen as the lectotype of the species.

Psammochromis schubotzi (Blgr.), 1914. Lakes Edward and George; see Greenwood (1973 : 183–8).

The possible relationship between *P. schubotzi* and *A. schubotziella* (see p. 9) suggested in that paper can no longer be upheld since the latter taxon shares none of the derived features shown by *P. schubotzi.*

Psammochromis riponianus (Blgr.), Lake Victoria and probably the Victoria Nile; see Greenwood (1960 : 252–6)

Psammochromis saxicola (Greenwood), 1960. Lake Victoria, and probably the Victoria Nile; see Greenwood (1960 : 256–9).

Psammochromis aelocephalus (Greenwood), 1959. Lake Victoria; see Greenwood (1959*b* : 214–17).

Psammochromis acidens (Greenwood), 1967. Lake Victoria, and probably the Victoria Nile; see Greenwood (1967 : 73–7).

Psammochromis cassius (Greenwood & Barel), 1978. Lake Victoria; see Greenwood & Barel (1978 : 161–4).

DISCUSSION

Previously (Greenwood, 1974 : fig. 70), most of the species included in *Psammochromis* were thought to be related to a lineage comprising, amongst other taxa, those now divided between the genera *Harpagochromis* and *Prognathochromis* (including its subgenus *Tridontochromis*); the *Psammochromis* species were considered to be most closely related to the latter group (the so-called *tridens* complex). In turn, the '*tridens* complex' and *Psammochromis* (then the '*riponianus* complex') were ranked as the sister group of a species (*H. welcommei*) here classified as the monotypic genus *Allochromis* (see p. 57).

Anatomical and osteological information now available for all these various taxa renders that hypothesis, based chiefly on neurocranial architecture, untenable in its entirety but not in part.

Skull form in *Psammochromis* is of a near-generalized type, and its derived dental features are unlike those in either subgenus of *Prognathochromis.*

The form of the dentary in *Psammochromis* exhibits apomorphies not shared with *Prognathochromis,* and there are no obvious synapomorphies linking *Psammochromis* with the dentally specialized *Allochromis* (the former *H. welcommei*).

However, there are certain derived features in the morphology of the dentary in *Psammochromis* which might still indicate its relationship with *Allochromis,* an argument which is taken up later (p. 60). These same features may also indicate a shared common ancestry with *Macropleurodus, Paralabidochromis* and *Ptyochromis* (see p. 66). In other words, *Psammochromis* and *Allochromis* together may constitute the sister group of the three other genera (see also pp 92–94).

Psammochromis acidens previously was given, tentatively, the status of sister group to the '*empodisma–obtusidens*' lineage, that is, the genus *Gaurochromis*; p. 32 (Greenwood, 1974).

Now that skeletal material of *P. acidens* is available it is clear that the lower jaw morphology in this species is far removed from that in *Gaurochromis.* Likewise, a possible relationship of *P. cassius* with the '*serranus* group' (that is, *Harpagochromis*), as suggested by Greenwood & Barel (1978 : 164), is not supported by the peculiar morphology of its lower jaw; both *P. acidens* and *P. cassius* have the distinctive and derived type of dentary characterizing the genus. *Psammochromis cassius* and *P. acidens* do, however, depart from other members of the lineage in having both a very different tooth form (see p. 54), and chest scales which are not noticeably smaller than those on the ventrolateral flanks and belly. The latter feature must be ranked as plesiomorphic, the dental one as derived. Possibly the two species together represent a subgroup within the lineage, but more material must be studied before they are formally recognized as such.

ALLOCHROMIS gen. nov.

TYPE SPECIES: *Haplochromis welcommei* Greenwood, 1966. Lake Victoria.

ETYMOLOGY. From the Greek '*allos*', different, strange + *chromis,* alluding to the unusual tooth shape and dental pattern, as well as to the lepidophagous habits of the type species.

DIAGNOSIS. Haplochromine fishes having an adult size range of *ca* 80–105 mm SL, a shallow, streamlined body (depth 30–33% SL), a gently decurved dorsal head profile (sloping at *ca* 35°–40°), a horizontal mouth and slightly thickened lips (Fig. 33). In general, the habitus is like that of many *Prognathochromis* species. *Allochromis* is, however, immediately distinguished by its dental morphology and the wide, broadly crescentic bands of fine teeth.

Teeth in the outer row of both jaws are close set and *have a very slender, tall and near-cylindrical neck which expands abruptly into a compressed, bicuspid crown which is about twice as broad as the neck; the crown and upper third of the neck are strongly recurved and lie almost at right angles to the rest of the tooth* (see Fig. 34). Inner row teeth are mostly tricuspid, the cusps of approximately equal size, and the whole crown strongly recurved.

Both jaws have the teeth arranged in a broad, almost crescentic band extending nearly to the posterior limits of the dentigerous surfaces involved (Fig. 35).

DESCRIPTION

Habitus (Fig. 33). A shallow, streamlined body combined with the gently curved and sloping head profile give this taxon a very *Prognathochromis*-like appearance (cf. Fig. 8). The mouth is horizontal and the lips are slightly thickened.

Adult size range for the few specimens known is *ca* 80–105 mm SL.

Neurocranium. Overall skull shape closely approaches that in species of the *Psammochromis* lineage; that is, a near-generalized neurocranium but with somewhat shallower otico-occipital and pre-orbital regions (*ca* 25% and 45% of neurocranial length, respectively). The supraoccipital crest is relatively low and wedge-shaped in profile.

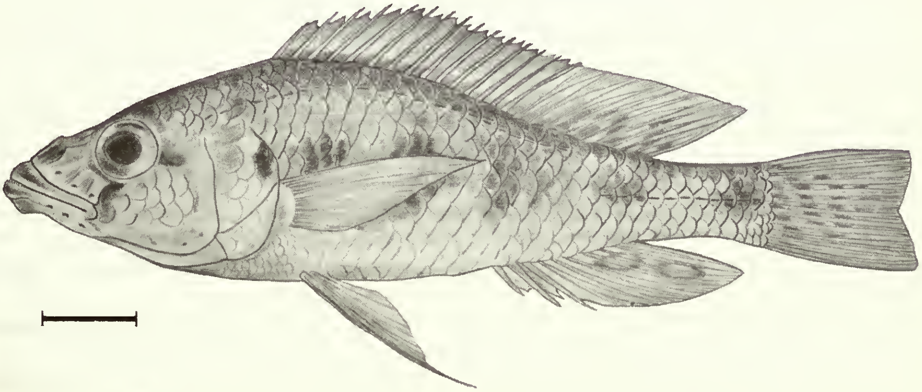

Fig. 33 *Allochromis welcommei.* Lake Victoria. Scale = 1 cm.

Dentition. Outer row teeth have a very characteristic shape and cusp form (see Fig. 34). In lateral view the tooth has a very slender, nearly cylindrical and tall neck which expands rather abruptly, but equally on either side, into a compressed bicuspid crown. The crown is almost twice as wide as the body of the tooth, its outline resembling a stylized drawing of a tulip. Both the crown and the upper third of the neck are strongly recurved.

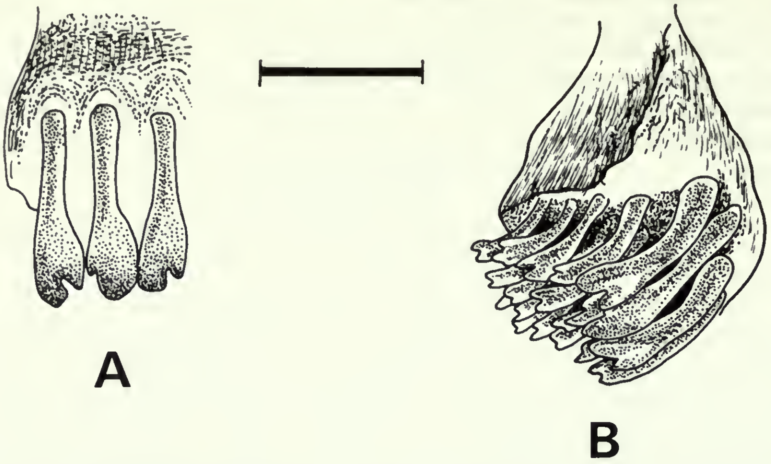

Fig. 34 Teeth from the left premaxilla of *Allochromis welcommei.* A. Labial aspect, viewed anteriorly. B. Ventromedial aspect viewed somewhat anteriorly. Scale = 1 mm.

Most outer teeth are unequally bicuspid, but there are a few tricuspids posteriorly in the row. The major cusp has a sub-acuminate, almost rounded distal margin; the minor cusp is more acute but is by no means pointed. In life these teeth, and those of the inner series, are moveably attached to the jaw.

Teeth in the inner series have the same overall shape as the outer ones but the crown is generally tricuspid, although bicuspids do occur frequently in the outermost row. There is little difference in the size of the three cusps, but the middle one is slightly higher and broader; their distal margins are sub-acuminate. All inner teeth are strongly recurved.

A very gradual size gradient exists across the inner rows; teeth in the outermost row are almost as tall as those in the outer series.

There are 70–80 close-set teeth in the outer premaxillary row, the margins of their cusps contiguous or slightly overlapping.

The dental pattern in both jaws is of a highly derived and distinctive type (see Fig. 35). The teeth are set out in broad crescentic bands which are not confined to the anterolateral parts of the jaw, but extend almost to the posterior limits of their respective dentigerous surfaces. Each arm of the crescent decreases gradually in width so that the inner tooth bands are multiseriate to their posterior limits in the dentary, and almost to those limits in the premaxilla (Fig. 35).

At its broadest point there are 7–11 rows in the upper, and 6–11 in the lower jaw, the numbers decreasing posterolaterally to *ca* 3 or 4 in the latter and a single or double row in the former. The rows are very closely spaced and there is no gap between the inner and outer tooth rows in either jaw.

Upper jaw. The premaxilla has the greater part of its dentigerous arms inflated and ovoid in cross section; the posterior quarter of each arm, however, is less enlarged and is more compressed.

The ascending processes are only about half as long as the horizontal dentigerous arms, which are produced anteriorly and anterolaterally into a slight but broad beak.

The maxilla is elongate and relatively shallow, its articular head with only a slight medial curvature.

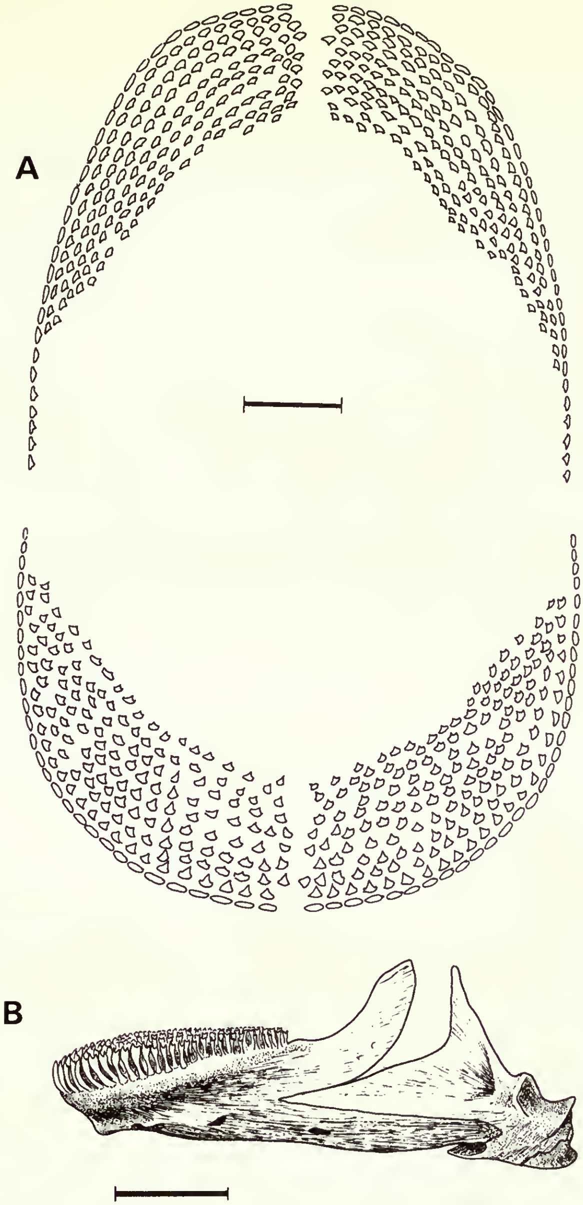

Fig. 35 A. Dental pattern of *Allochromis welcommei.* Scale = 1 mm. B. Dentary of *Allochromis welcommei,* in lateral view. Scale = 3 mm.

Lower jaw. The dentary is elongate and relatively shallow. Its alveolar surface, however, is inflated and broad, forming a deep bullation extending beyond, and overhanging, the lateral wall of each ramus. Anterolaterally, the inflated region extends almost to the ventral margin of the ramus.

Each alveolar surface has a decided anteroventral inclination, sloping forwards and downwards from a point immediately in front of the ascending dentary arm to the superficially shallow symphysial area. The symphysis itself extends vertically through the bullation so that it is both deep vertically and, since it incorporates the bullate part of the bone, also wide dorsally.

The anguloarticular is of the generalized type, with an acute tip to its horizontally aligned ventral limb.

Lower jaw length is 41–46% of head length, and the jaw is clearly longer (1·3–2·0 times) than broad.

Lower pharyngeal bone and teeth. The bone is slender and relatively elongate, its triangular dentigerous surface slightly broader than long (see Greenwood, 1966 : fig. 6). Apart from the transverse posterior row, none of the pharyngeal teeth is noticeably enlarged; all are small, compressed and weakly cuspidate.

Contained species

Allochromis welcommei (Greenwood), 1966. Lake Victoria; see Greenwood (1966 : 309–18).

DISCUSSION

There are no synapomorphic features which allow the sister taxon of *Allochromis* to be identified precisely.

The outer row jaw teeth in *Allochromis* are unique and thus autapomorphic, but the multiseriate dental pattern does occur in several lineages (*Hoplotilapia, Platytaeniodus, Neochromis* and *Ptyochromis,* especially *P. xenognathus*). However, *Allochromis* does not exhibit other characteristics which can be considered unequivocally synapomorphic with those in any of these taxa, and each, including *Allochromis,* has its own distinctive dental pattern when these are compared in detail. One apparent synapomorphy, the inflated premaxillary dentigerous arms, would seem to be a parallelism associated either with the presence of enlarged teeth, a multiseriate dentition, or a combination of both (see discussion on p. 52).

Allochromis also differs from most of the taxa mentioned above in the gross morphology of its neurocranium, which does, however, resemble that in *Psammochromis.* In both genera the skull deviates from the generalized condition towards that found in the least derived species of the *Prognathochromis* lineage. It was this similarity in skull architecture which previously led me (Greenwood, 1974) to suggest that *Allochromis* was the sister group of the '*tridens* complex' (now recognized as the subgenus *Tridontochromis* of *Prognathochromis*; p. 20). A reconsideration of other derived features in both *Allochromis* and *Prognathochromis, sensu lato,* now renders that hypothesis untenable.

In that paper, I also suggested that *A. welcommei* (plus the '*tridens* complex') might be the sister group of three taxa which, together with others, now constitute the genus *Psammochromis*; see above, p. 56.

Certain neurocranial similarities existing between *Allochromis* and *Psammochromis* have already been noted (p. 57), but more significant (particularly considering the very different tooth form and patterns in the genera) are their similarities in lower jaw morphology, which is undeniably derived in both taxa.

Both genera have a pronounced anteroventral inclination to the outer tooth row of the dentary (itself a slender, elongate bone), whose anterior and anterolateral aspects are markedly inflated below the alveolar surface. The tooth rows in *Psammochromis* are neither as numerous nor as spatially extensive as they are in *Allochromis* so that those shared derived features cannot be ascribed to that cause, and thus be dismissed as parallelisms.

If these apparent synapomorphies in the morphology of the dentary can be accepted as truly synapomorphic, *Allochromis* could be the derived sister taxon of *Psammochromis.* If, in turn, one can accept the arguments put forward for a common ancestry shared by *Psammochromis* on the one hand and *Paralabidochromis, Ptyochromis* and *Macropleurodus* on the other (see p. 66), then *Psammochromis* and *Allochromis* together should comprise the sister group of the other three genera combined. Another possible member of this lineage *sensu lato, Schubotzia eduardiana,* is discussed on pp. 87–88 & 94.

PTYOCHROMIS gen. nov.

TYPE SPECIES: *Ctenochromis sauvagei* Pfeffer, 1896. Lake Victoria (see Greenwood, 1957 : 76–81, plate 4, upper figure).

Etymology. From the Greek '*pyto*', to spit out, + *chromis*, alluding to the way in which these fishes crush mollusc shells orally and then spit out the fragments.

Diagnosis. Haplochromine fishes with a maximum adult size range of 105–130 mm SL, a dorsal head profile ranging from straight and steeply sloping to strongly decurved, a small,

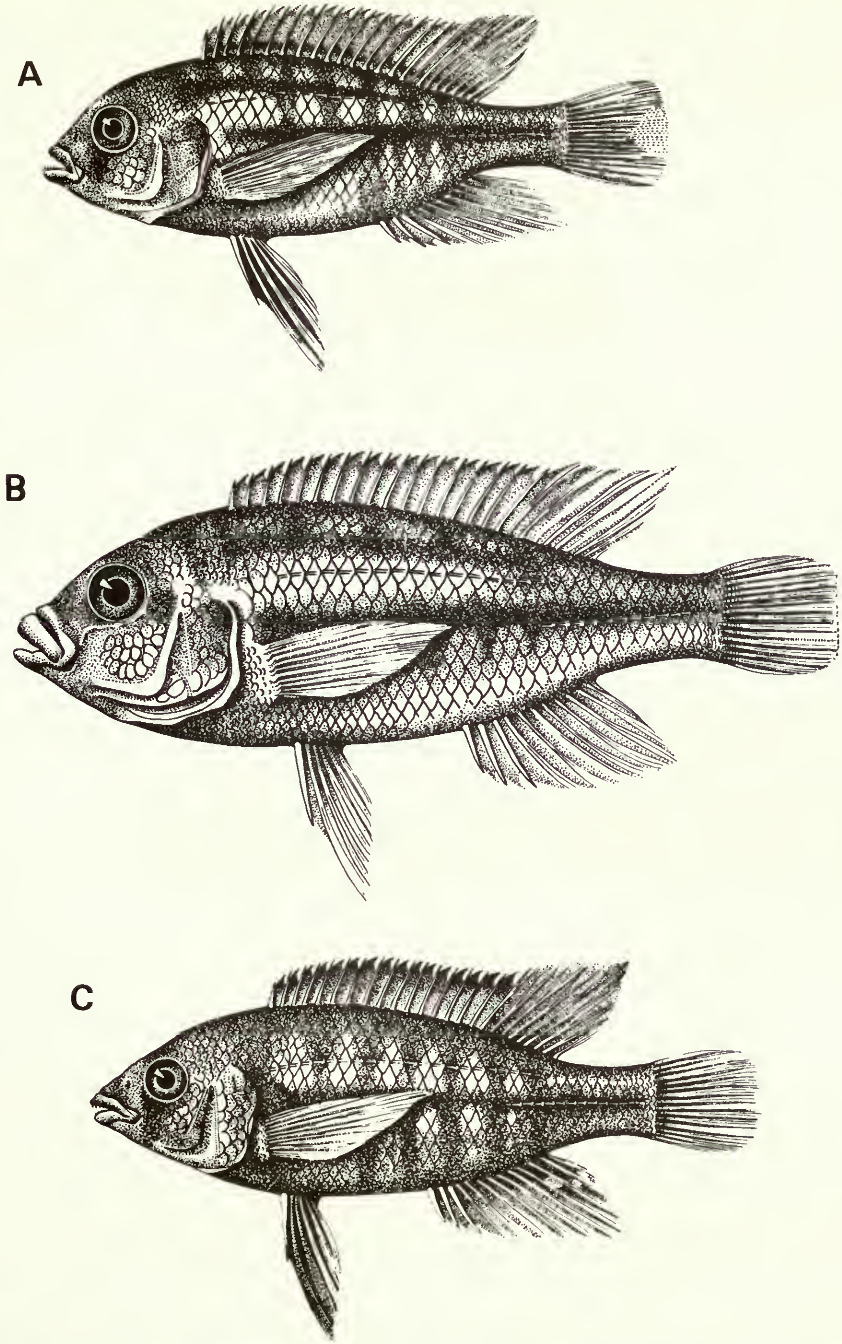

Fig. 36 A. *Ptyochromis sauvagei*. Lake Victoria. About natural size. B. *Ptyochromis granti*. Lake Victoria. About two-thirds natural size. C. *Ptyochromis xenognathus*. Lake Victoria. About natural size.

horizontal mouth with thickened lips, and a *lower jaw* that is *usually shorter than the upper. The slender teeth are very strongly recurved, those of the inner series arranged in a broad band across the anterior part of each jaw.*

Neurocranium with the preorbital face sloping fairly steeply (*ca.* 60°–65°, but 70°–75° in one species), *its preorbital depth 30–33% of neurocranial length.*

Premaxilla with somewhat inflated dentigerous arms which, anteriorly, are produced into a broad, shelf-like 'beak'. *Twenty-six to 56 teeth in the outer premaxillary row (modal range 40–44).*

Dentary deep posteriorly but shallowing rapidly over the anterior two-thirds of its length, the lateral walls curving abruptly mediad from a level immediately below the alveolar surface. The outer margin of this surface, over its anterior half, dips downwards and slightly outwards so that the insertions of the outer row of teeth lie below those of the inner series.

Lower jaw length 22–38% of head length (modal range 34–35%).

Lower pharyngeal bone stout and broad, the median rows with coarser teeth, but none is submolariform or molariform.

DESCRIPTION

Habitus (Fig. 36). The dorsal head profile is variable, both inter- and intraspecifically, and ranges from strongly decurved to straight but steeply sloping. The mouth is horizontal, or less commonly, slightly oblique. There is a tendency for the lower jaw to be slightly shorter than the upper one; the lips are thickened, more so in some species than in others.

Body form shows no outstanding features, and is of the generalized type.

Maximum adult size ranges from 105–130 mm SL; sexual maturity is reached at lengths between 70 and 100 mm.

Neurocranium. Skull form in this genus combines features seen in *Macropleurodus* and *Paralabidochromis* (see pp. 81 & 68) but with most species and individuals approximating more closely to the latter condition (Fig. 37). Generally, the preorbital face slopes fairly steeply (*ca* 60°–65° to the horizontal) but in one species (*P. annectens*) the slope may reach 70°–75°; preorbital skull depth ranges from 30–33% of neurocranial length. The tip of the vomer lies distinctly below the level of the parasphenoid.

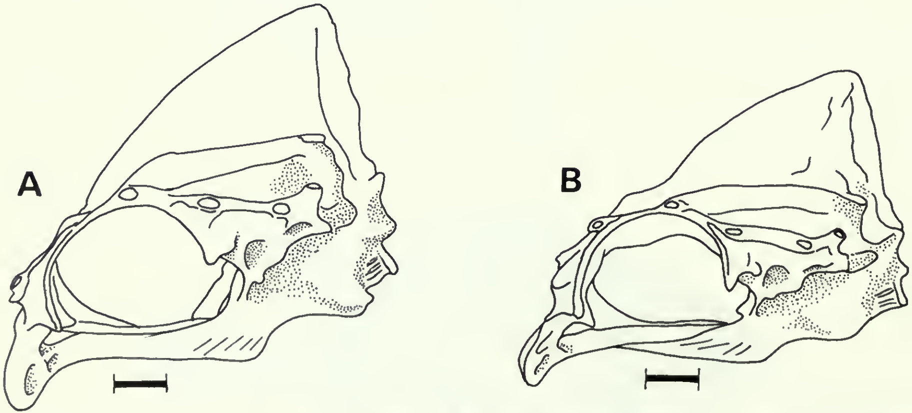

Fig. 37 Neurocranium (in left lateral view) of A. *Ptyochromis annectens*, and B. *Ptyochromis xenognathus*. Scale = 3 mm.

Supraoccipital crest outline varies from near pyramidical to a deep wedge-shape, with a corresponding variation in the height of its posterior margin.

Dentition. In both jaws the teeth in the outer row are slender but strong, with markedly recurved crowns (Fig. 38); the angle formed between the buccal face of the crown and the neck is *ca* 130°. The crown is neither expanded nor noticeably compressed, and joins imperceptibly the cylindrical neck.

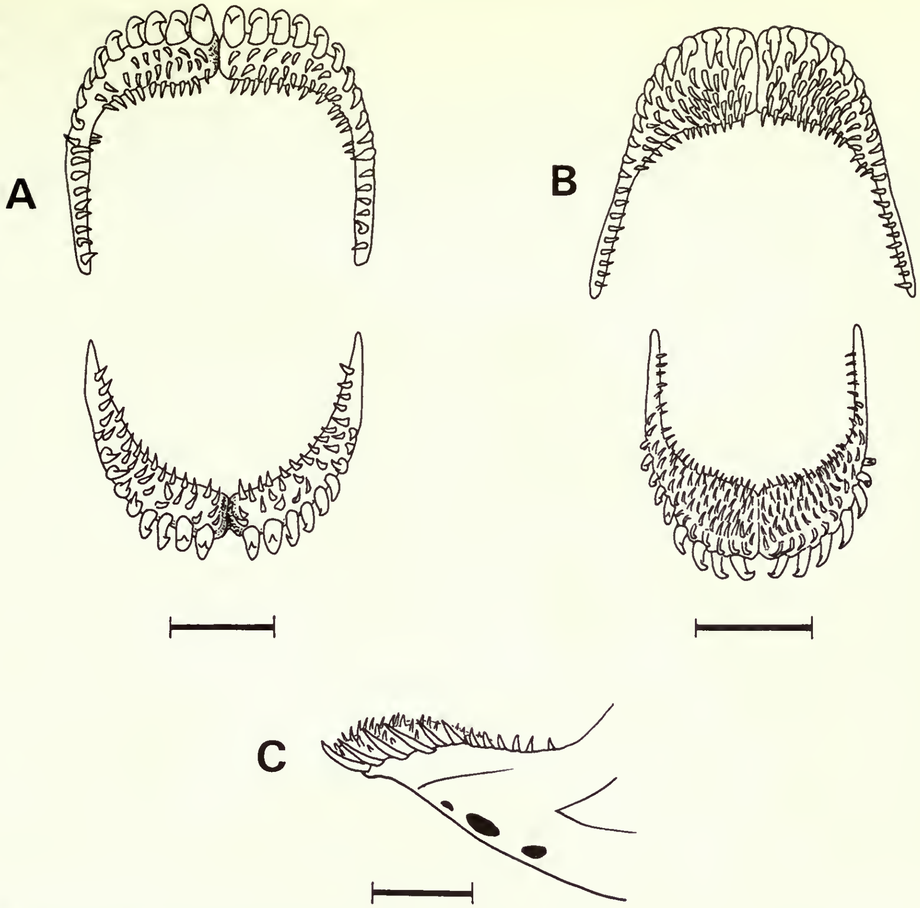

Fig. 38 Dental pattern in: A. *Ptyochromis annectens*, B. & C. *P. xenognathus* (entire pattern, and as seen laterally in dentary respectively). Scale = 3 mm.

Unequally bicuspid crowns predominate in the denition of fishes <80 mm SL; a mixture of bi- and unicuspids occurs in fishes between 80 and 100 mm long (with unicuspids first appearing anteriorly in the jaws). In larger individuals the teeth are all or predominantly unicuspid.

Anteriorly and anterolaterally in the lower jaw the teeth are implanted almost procumbently and below the level of those situated laterally (see also the description of the dentary, p. 64). As a result, their crowns are on about the same level as those of the inner teeth. Tooth insertion on the premaxilla is nearly vertical or very slightly procumbent.

There are 26–56 (modal range 40–42) teeth in the outer premaxillary row.

Teeth forming the inner rows are small and arranged in a characteristic pattern, namely a wide anteromedial band lying transversely across the front of each jaw, but narrowing abruptly to a single or double row laterally, and a single row posterolaterally (see Fig. 38A). Modally, there are 4 or 5 rows in the upper jaw and 3 or 4 in the lower; *Ptyochromis xenognathus* (Fig. 38B) is exceptional in having modes of 7 and 5 rows in the jaws respectively. The total range of tooth row numbers is from 3–9 (rarely 2) in the premaxilla and 2–9 in the dentary (see Greenwood, 1957 : 83 for comments on the aberrant tooth pattern in the holotype of *P. annectens*; also Regan, 1922 : fig. 14).

Most inner teeth in fishes less than 80 mm SL are tricuspid, but are predominantly unicuspid in fishes >90 mm SL.

Upper jaw. Three of the four *Ptyochromis* species have the dentigerous arms of the premaxilla somewhat inflated, especially anteriorly and anterolaterally where the tooth rows are broadest. The fourth species (*P. xenognathus*), has little or no inflation of the arms, but anteriorly (in the region below the ascending processes) the bone is extended forward as a shallow but broad shelf corresponding with the area of maximum tooth row width. (This species, it will be recalled, has the highest number of inner tooth rows.) Because this shelf extends forwards as a plateau beneath the ,ascending processes, the premaxilla in *P. xenognathus* has very characteristic lateral and dorsal profiles (Fig. 39).

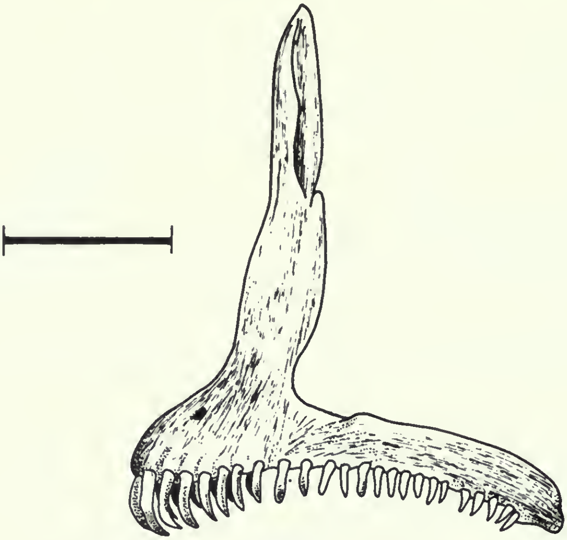

Fig. 39 Premaxilla (left) of *Ptyochromis xenognathus*. Scale = 3 mm.

Anterolaterally, each dentigerous arm of the premaxilla curves rather sharply mediad so that in occlusal view the entire structure has the outline of a broad-based U; the base is narrowest in *P. xenognathus.*

Premaxillary ascending processes are shorter than the dentigerous arms in all species except *P. xenognathus,* where they are equal.

Each maxilla is foreshortened, its posterior arm relatively deep, with a strongly concave median face (and a corresponding bullation of its lateral face). There is some variation in the extent to which the articulatory head is curved medially; curvature is strong in *P. granti* and *P. annectens,* but only moderate in *P. sauvagei* and *P. xenognathus.*

Dentary. There are several outstanding, and derived, features in this bone. In all species it is deep posteriorly but shallows rapidly forward from the region near the point where the ascending (coronoid) arm begins to rise. Consequently, in lateral view the ventral profile of the dentary appears to slope steeply upwards into a shallow symphysial region (Fig. 40). Anteriorly, when compared with the condition seen in both generalized and differently derived dentaries, the side wall of the dentary in *Ptyochromis* species does not descend vertically for some distance before it begins to curve inwards. Instead, its medially directed curvature begins only a short distance below the alveolar surface, and the curvature is unusually abrupt. This pattern of curvature, coupled with the relatively deep coronoid region of the bone, gives the dentary a very characteristic appearance (Fig. 38C). The appearance is most extreme in *P. xenognathus* and is least marked in *P. sauvagei* and *P. granti.* Parenthetically it should be noted here that the dentary of *P. annectens* figured in Greenwood (1974 : 70, fig. 40, captioned *Haplochromis prodromus,* but see p. 66 below for nomenclature) was in fact drawn from a misidentified skeleton of a *Paralabidochromis* species (see p. 67), probably *Paralabidochromis crassilabris.*

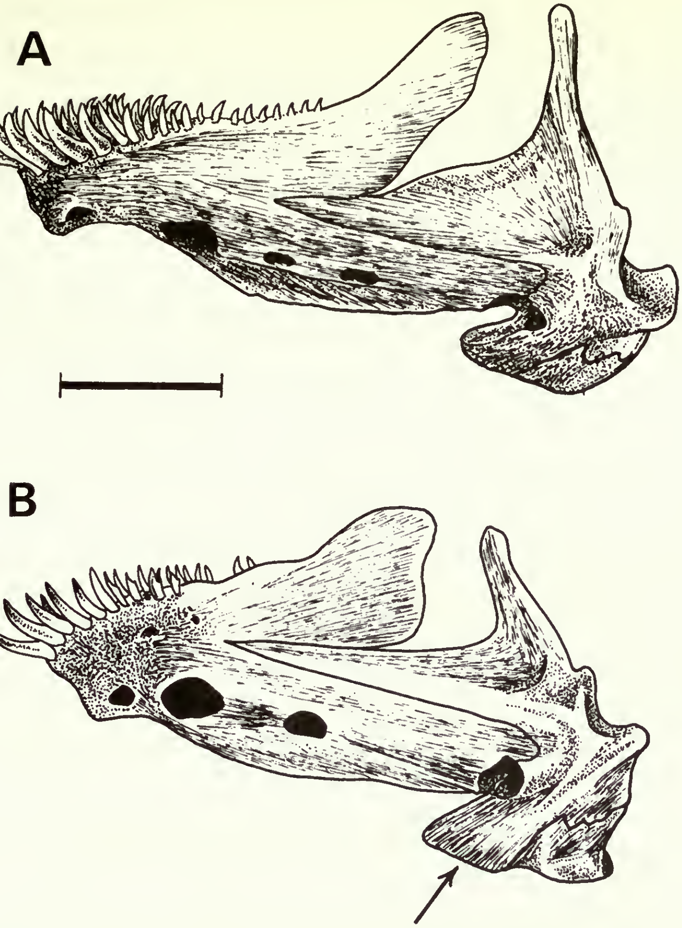

Fig. 40 Left dentary of: A. *Ptyochromis sauvagei* seen in lateral view. B. *Ptyochromis xenognathus*, viewed somewhat ventrolaterally, from the left, to show the shape of the anterior margin to the anguloarticular (arrowed). Scale = 3 mm.

Anteriorly and anteromedially the alveolar surface of the dentary has a noticeable fore-and-aft expansion (corresponding, as in the premaxilla, to the greatest width of the inner tooth rows), and a correlated antero-posterior lengthening of the symphysial surface.

About halfway along its length the alveolar surface for the outer tooth row in the dentary dips downwards and forward to occupy a position below the alveolar surface for the inner tooth rows. Immediately below the somewhat ventrolaterally displaced anterior outer teeth, the dentary is thickened and a little bullate. A similar swelling, associated with a displaced outer tooth row, occurs in *Psammochromis* (see p. 55 and further discussion on p. 66).

The anguloarticular is deep and stout. Its anteroventral arm, which barely underlies the posteroventral edge of the dentary, has a blunt anterior margin (Fig. 40).

Lower jaw length is 22–38% head length (modal range 34–35%) and is thus shorter than in a generalized syncranium but comparable with that in some derived lineages (eg *Paralabidochromis* and *Macropleurodus*). Usually the lower jaw is longer than broad (1·3–1·4 times longer).

Contained species

The taxa are listed in order of their increasing derivation.

Ptyochromis sauvagei (Pfeffer), 1896. Lake Victoria; see Greenwood (1957 : 76–81).

Ptyochromis annectens (Regan), 1922. Lake Victoria; see Greenwood (1957 : 82–6) where the species is referred to as *Haplochromis prodromus* Trewavas, 1935. *Ptyochromis annectens* was originally described by Regan (1922) as *Haplochromis annectens* but when Trewavas (1935) transferred the Lake Malawi species *Cyrtocara annectens* Regan, 1921 to the genus *Haplochromis,* she proposed the replacement name *prodromus* for the then homonymous Victoria taxon. With the removal of Regan's 1922 species from the genus *Haplochromis,* his original specific epithet again becomes available.

Ptyochromis granti (Blgr.), 1906. Lake Victoria; see Greenwood (1957 : 86–90).

Ptyochromis xenognathus (Greenwood), 1957. Lake Victoria; see Greenwood (1957 : 90–5).

Discussion

In an earlier review of relationships amongst Lake Victoria haplochromine species (Greenwood, 1974, fig. 70), the four species now referred to *Ptyochromis* were also grouped together, and with the addition of two species currently placed in *Paralabidochromis* (p. 71), were considered to be the sister group of *Macropleurodus.*

Both *Ptyochromis* and *Macropleurodus* share certain derived features in the morphology of the lower jaw, namely an outer tooth row dipping ventrally over the anterior half of its length, a deep and stout anguloarticular complex whose anteroventral arm has an obtuse anterior margin, and a dentary whose lateral walls, at least anteriorly, are abruptly curved inwards from almost the level of the alveolar surface, so that they are aligned more nearly horizontally than vertically.

Dentally, there is little in common between the two lineages (cf. pp. 62 & 82), except for the strongly recurved tooth form in both. Certainly the teeth in two *Paralabidochromis* species (see p. 69) more closely resemble those of juvenile *Macropleurodus* than do the teeth in any *Ptyochromis* species.

All the derived jaw features shared by *Ptyochromis* and *Macropleurodus* are also present in *Paralabidochromis* (see pp. 64, 70 & 83) although the inward slope of the dentary wall is less well-developed in that lineage.

Trophically, both *Ptyochromis* and *Macropleurodus* share a derived feeding habit, that is, the oral removal of a snail's shell before its soft parts are ingested (see Greenwood, 1974 : 69 *et seq.*). *Paralabidochromis* species, on the other hand, are all insectivores with some taxa known to be specialized in their ability to remove insect larvae and pupae from burrows in wood or rock (Greenwood, 1959*b* : 210).

In brief, *Ptyochromis, Macropleurodus* and *Paralabidochromis* all share a number of derived features in the jaws and detailed morphology of their jaw bones (especially the lower jaw), and in the way the outer row of teeth is inserted on the dentary. All have a similar and derived neurocranial form. The teeth and the dental pattern are derived in all three genera, with those of *Ptyochromis* and *Paralabidochromis* more alike than either is to *Macropleurodus* which has the most derived tooth morphology and dental pattern (see p. 82).

From the evidence available it is impossible to indicate precise interrelationships between the three genera, although the original concept of their being more closely related to one another than to any other lineage (Greenwood, 1974) does seem to be corroborated by the characters discussed above and on p. 84. (See also p. 95).

The peculiar alignment of the outer tooth row in the dentary in these genera resembles closely that of *Psammochromis* (see p. 55). There is a further resemblance in the way the anterior wall of the dentary immediately below the displaced section of the tooth row is thickened and bullate. In other respects, however, the morphology of the dentary (and its anguloarticular bone) in *Psammochromis* is near the elongate and shallow generalized type, and not like the relatively deep, short and stout bone in *Macropleurodus, Paralabidochromis* and some *Ptyochromis* species. But, in two *Ptyochromis* (*P. sauvagei* and *P. xenognathus*) the proportions of the dentary are intermediate between those of *Psammochromis* and the dentary in the other *Ptyochromis* species. In turn, these other *Ptyochromis* species intergrade with the *Paralabidochromis* and *Macropleurodus* conditions, so that there is, in effect, a morphocline in dentary proportions running from *Psammochromis* to *Macropleurodus* (as representatives of the two extreme conditions).

The slender but strong, tall and recurved outer jaw teeth in *Psammochromis* must be ranked as derived in relation to the unequally biscuspid, slightly recurved and stout teeth characterizing many lineages. Basically, the *Psammochromis* tooth-form aproaches that of *Ptyochromis,* albeit one less strongly recurved and with the crown more obviously compressed. They could, however, be considered the plesiomorph 'sister form' of the *Ptyochromis* type.

Neurocranial shape in *Psammochromis* differs quite markedly from that in the other three genera under consideration (see p. 54); it represents a slight departure from the generalized type towards that of the predatory piscivorous lineage *Prognathochromis.* That is, a slight overall elongation and streamlining of the basic form, as compared with the foreshortening and elevation of that type manifest in *Ptyochromis, Paralabidochromis* and *Macropleurodus.*

Considering the various synapomorphies discussed above, their range of expression and their differences, *Psammochromis* could be included as a member of an assemblage forming the sister group of *Ptyochromis, Paralabidochromis* and *Macropleurodus* combined. In most respects the level of derivation (from their hypothetical common ancestor) which *Psammochromis* has reached, appears to be much less marked than that shown by any other member of the total assemblage.

PARALABIDOCHROMIS Greenwood, 1956

TYPE SPECIES: *Paralabidochromis victoriae* Greenwood, 1956. Lake Victoria.

Note. Regan (1920:45) erected the genus *Clinodon* for the species *Hemitilapia bayoni* Blgr, 1908. The paratype of that species, which Regan examined, was later chosen as the holotype for *Haplochromis plagiodon* Regan & Trewavas (1928:224–5), a species which I now include in the genus *Paralabidochromis.* Since the holotype of *Hemitilapia bayoni* Blgr., (see Boulenger, 1915: 491, fig. 340) the designated type species of Regan's *Clinodon* is, however, referrable to *Haplochromis obliquidens* (see Greenwood, 1956*b*: 226–232, and 1979:278), the older name *Clinodon* is not available for the taxon here called *Paralabidochromis.*

DIAGNOSIS. Haplochromines with a maximum adult size range of 70–150 mm SL, *a forceps-like dentition (lower teeth implanted procumbently),* lips somewhat thickened (hypertrophied and lobate in one species), mouth horizontal, dorsal head profile straight, or slightly concave, and sloping fairly steeply.

Neurocranium with a deep preorbital region (33–37% neurocranial length cf. 25–30%, *modal range 26–27% in the generalized skull);* entire preorbital gently curved and sloping at an angle of 45°–50°. Supraoccipital crest of variable outline, from near pyramidical to deeply wedge-shaped.

Dentary foreshortened and deep, with a marked lateral bullation in the region of its division into coronoid and horizontal arms. *Profile of the symphysial region with a pronounced posteroventral slope giving the jaw a distinctly chinless appearance. Lower jaw length 30–49% head length (modal range 33–35%).*

Premaxilla with slightly inflated dentigerous arms (oval in cross-section), its ascending processes as long as, or slightly longer than dentigerous arms. *Maxilla foreshortened,* its posterior arm deep but not markedly bullate.

Outer jaw teeth strong, slender, recurved and cylindrical in cross-section, the crown somewhat compressed when bicuspid, otherwise cylindrical. Teeth anteriorly and anterolaterally in the lower jaw implanted procumbently, sloping forwards and upward at an angle of *ca* 45°–50°. Upper jaw teeth implanted almost vertically, but when the premaxilla is *in situ* they are inclined forwards to form, with the procumbent lower teeth, a forceps-like dentition. *Relatively few outer teeth in both jaws,* 16–48 (modal range 30–35) in the premaxillary outer row. Cusp form variable but usually bicuspid in fishes <65–70 mm SL, and unicuspid, near conical in larger individuals.

Inner teeth arranged in 2 or 3 (rarely 1 or 4) rows, separated from the outer row by a distinct interspace.

Lower pharyngeal bone short and broad, the median row teeth coarse but rarely submolariform.

DESCRIPTION

Habitus (Fig. 41). Body form departs but slightly from the generalized *Astatotilapia* shape, with the dorsal head profile straight or slightly concave and sloping fairly steeply. The lips are somewhat thickened in all species and are hypertrophied, even lobate, in *P. chilotes.*

Maximum adult size range is from *ca* 70–150 mm SL.

Neurocranium. Skull form departs somewhat from the generalized condition in that the preorbital region is relatively deeper (33–37% neurocranial length, **cf.** 25–30%, modal range 26–27%) and in consequence the preorbital profile slopes more steeply (*ca* 45°–50°) and is slightly curved (Fig. 42). The supraoccipital crest is a little higher relative to the generalized condition, and varies in profile from pyramidical to deeply wedge-shaped.

Dentition. The outer jaw teeth are strong and robustly slender, recurved, and cylindrical in cross-section, the crown slightly compressed when bicuspid. Teeth anteriorly in the lower jaw are implanted procumbently so that they slope forward and upward at an angle of *ca* 45°–50° to the horizontal. All species have the anterior and immediately anterolateral

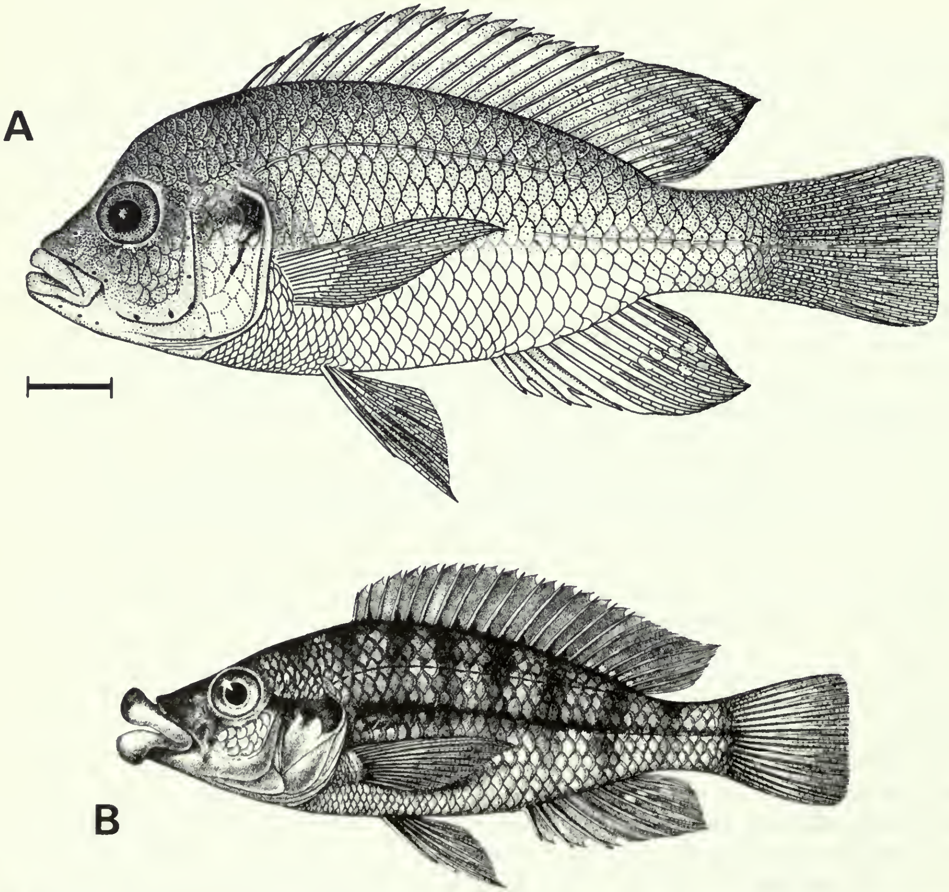

Fig. 41 A. *Paralabidochromis labiatus.* Lake George. Scale = 1 cm. B. *Paralabidochromis chilotes.* Lake Victoria. About two-thirds natural size.

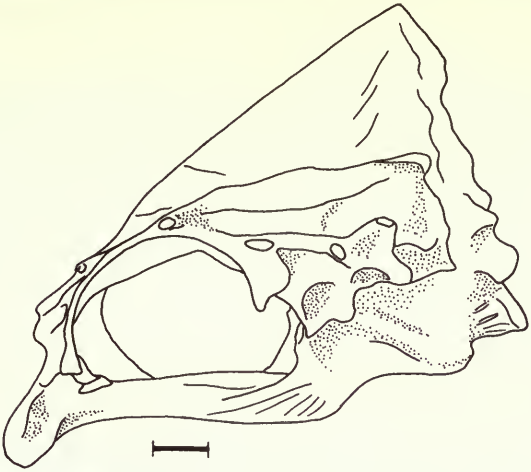

Fig. 42 Neurocranium (left lateral view) of *Paralabidochromis chilotes.* Scale = 3 mm.

teeth longer than the lateral ones; the size discrepancy being more marked in some species than in others. Since anteriorly the line of insertion for these outer teeth has a distinctly ventral direction, their tips lie at about the same level as those of the inner rows.

The upper teeth are inserted almost vertically on the premaxilla, but when that bone is *in situ* it slopes at an angle such that the anterior upper teeth are directed procumbently, and they occlude with their counterparts in the lower jaw to provide a forceps-like dental arrangement.

In most species the dental arcade in both jaws, but particularly that in the premaxilla, narrows anteriorly to give it a narrow-based 'U'-shaped outline.

There are relatively few teeth in the outer row of either jaw, the premaxillary series having 16–48 (modal range 30–35).

Cusp form is interspecifically variable, but is predominantly bicuspid in most specimens of all species at a standard length of less than 65–70 mm.

Species in which the definitive outer dentition is unicuspid have a near-conical tip to the crown, which is thus more robust than in the typical unicuspid teeth in such lineages as *Harpagochromis* and *Prognathochromis.*

In one species, *P. victoriae,* the anterior teeth in both jaws are more slender and are relatively longer than those in other members of the genus, thus enhancing the forceps-like nature of the dentition (see Greenwood, 1956*a* : 328, and fig. 10).

Two types of bicuspid teeth occur in *Paralabidochromis.* The commoner is close to the generalized kind but has the cusps of markedly unequal size, the major one approximately equilateral in outline and less compressed than in the generalized tooth; the minor cusp may be relatively smaller in *Paralabidochromis* teeth. The second cusp type has so far been recorded, as the predominant form, in only one species, *P. plagiodon.* Here the minor cusp is aligned at a slight angle so that it resembles a weak spur, and the posterior margin of the major cusp slopes obliquely forward to meet its near vertical anterior margin at a somewhat obtuse angle; the entire cusp is also more compressed than in the other type of tooth (Fig. 43). In other words, cusp form in *P. plagiodon* resembles that in *Haplochromis lividus* (Greenwood, 1956*b* : fig. 2B; 1959 : 206; and 1979 : 278), although it is stouter overall and the anterior angle of the major cusp lies in the same vertical as the neck of the tooth (not outside it as in *Haplochromis*).

Unlike the generalized bicuspid, where the crown is expanded relative to the neck, in neither type of *Paralabidochromis* tooth is the crown much wider than the neck.

Inner teeth are tricuspid (sometimes weakly so) or, in specimens >90 mm SL, a mixture of tri- and unicuspids. They are arranged in 2 or 3 rows (rarely in 1 or 4 rows), and are always

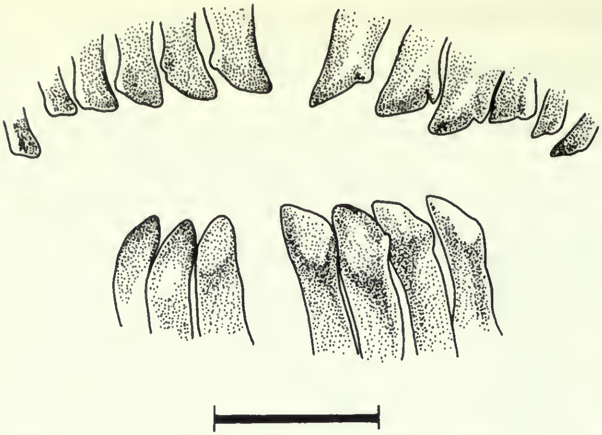

Fig. 43 Outer jaw teeth of *Paralabidochromis plagiodon*, viewed *in situ* and from in front, to show the nature of the crowns. Since the lips are not fully reflected, the bases of the teeth are not visible. Scale = 1 mm.

separated from the outer teeth by a distinct interspace; in some individuals the outermost inner row is composed, anteriorly, of teeth slightly larger than those of the other inner rows, but still distinctly smaller than the outer row teeth.

Mouth. The lips are thickened in all *Paralabidochromis* species and are hypertrophied in *P. chilotes*; some individuals of that species have both lips produced into prominent medial lobes, but in others the lobes may be represented only by a slight bulbous swelling (see Greenwood, 1959*b* : 208, and fig. 11). The mouth is horizontal, and both jaws are equal anteriorly.

Upper jaw. The dentigerous arms of the premaxillae are somewhat inflated, especially anteriorly and anterolaterally (where the bone is a compressed oval in cross section). Inflation is more marked in some species than in others. The ascending processes are as long as, or slightly longer than the dentigerous arms.

The maxilla is foreshortened and its posterior arm is relatively deep; the medial face of the latter is not markedly concave and thus there is no strong bullation of its lateral aspect. The articular head of the bone curves gently mediad.

Lower jaw. The dentary is short and deep, giving the entire lower jaw a foreshortened appearance (Fig. 44). This impression is enhanced by the bullation of each ramus near its

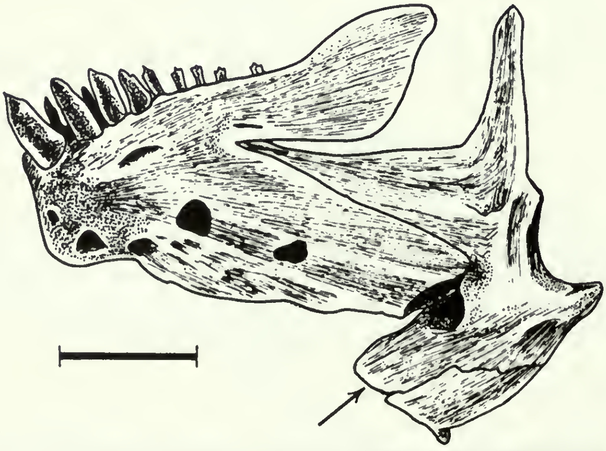

Fig. 44 Lower jaw of *Paralabidochromis crassilabris*, seen ventrolaterally from the left, to show the anterior margin of the anguloarticular (arrowed). Scale = 2 mm.

division into ascending (coronoid) and horizontal limbs. In these respects the dentary resembles that found in some other lineages (eg *Lipochromis, Neochromis* and *Macropleurodus*).

Its anterior profile, both in lateral and in ventral views, is most characteristic. The symphysial region of the bone has a pronounced posteroventral slope which gives it a rather 'chinless' look in lateral view. This area is also slightly expanded horizontally and the bone hereabouts is noticeably thickened. Anteriorly, each ramus has only a gently curved mediad inclination so that the entire jaw, when viewed from above, has a bluntly apexed V-shaped outline. In all these respects the dentary of *Paralabidochromis* is unlike that in *Lipochromis* and *Neochromis,* and in most respects that of *Macropleurodus* as well; see above.

In three species (*P. crassilabris, P. plagiodon* and *P. beadlei*) the lateral wall of each ramus has, anteriorly, a fairly marked mediad curvature so that it slopes inwards rather than almost vertically downwards (see also *Ptyochromis* and *Macropleurodus,* pp. 64 & 84 respectively).

The anguloarticular is deep and robust, the anterior point of its anteroventral arm blunt or rectangular in outline (Fig. 44).

Lower jaw length ranges from 30–49% of head length (modal range 33–35%); the jaw is always narrower than it is long. In both these features *Paralabidochromis* broadly overlaps the majority of non-piscivorous lineages whose adults have a maximum length of less than 115 mm, but its modal lower jaw length is slightly lower.

Lower pharyngeal bone and dentition. The bone is short and broad, its triangular dentigerous area always broader than it is long. All but two species have the median tooth rows composed of coarse teeth, and in some individuals of certain species these teeth (especially the posterior few) have submolariform crowns; otherwise the crown is bicuspid and compressed.

Contained species

The taxa are grouped, approximately, in order of their related and increasing derivation.

Paralabidochromis beadlei (Trewavas), 1933. Lake Nabugabo; see Greenwood (1965: 335–41).

Paralabidochromis paucidens (Regan), 1921. Lake Kivu; see Regan (1921: 638).

Paralabidochromis crassilabris (Blgr.), 1906. Lake Victoria; I have not yet published a revised description of this species; the information used here is derived from the specimens used by Regan (1922: 167–8) in his previous revision, supplemented by new material and osteological preparations.

Paralabidochromis labiatus (Trewavas), 1933. Lakes Edward and George; see Greenwood (1973: 196–9).

Paralabidochromis plagiodon (Regan & Trewavas), 1928. Lake Victoria; see Greenwood (1959*b*: 205–7); and note on p. 67 above.

Paralabidochromis chromogynos (Greenwood), 1959. Lake Victoria; see Greenwood (1959*b*: 212–4).

Paralabidochromis chilotes (Blgr.), 1911. Lake Victoria and probably, the Victoria Nile; see Greenwood (1959*b*: 207–12).

Paralabidochromis victoriae Greenwood, 1956. Lake Victoria; see Greenwood (1956*a*: 328–9).

DISCUSSION

Paralabidochromis victoriae has the most derived and forceps-like dentition of all the species, yet morphologically speaking, the various stages in its evolution are represented in other members of the lineage. The least derived conditions are those seen in *P. beadlei* (Lake Nabugabo), *P. paucidens* (Lake Kivu) and *P. labiatus* (Lake Edward and George) and *P. crassilabris* (Lake Victoria). Two Lake Victoria species *P. chromogynos* and *P. chilotes*, in that order, most closely approach *P. victoriae*.

Paralabidochromis plagiodon, although retaining a basically plesiomorph tooth form for a member of this lineage (but a distinctly apomorph one relative to the basic bicuspid tooth) does exhibit certain autapomorphic features in the crown shape of these teeth (see p. 69 above). The expansive, obliquely margined major cusp, the small spur-like minor cusp, and the somewhat buccally orientated crown (Fig. 43) set *P. plagiodon* apart from other members of the lineage (with which it nevertheless shares several synapomorphies).

Its distinctive dental features, however, do approach those seen in small specimens (< 90 mm SL) of *Macropleurodus*, a genus which differs from *Paralabidochromis* in several autapomorphic dental characters and some osteological ones as well. The *Macropleurodus*-like features in the dentition of *P. plagiodon*, together with certain derived features in the morphology of the lower jaw shared by *Macropleurodus* and all species of *Paralabidochromis*, suggest that the lineages could have shared a relatively recent common ancestry. This, and other possible interrelationships of *Paralabidochromis*, are discussed further on pages 66, 84 & 93.

HOPLOTILAPIA Hilgendorf, 1888

TYPE SPECIES (*Paratilapia*?) *retrodens* Hilgendorf, 1888. Lake Victoria; see Greenwood (1956*a*: 319 & 321) for detailed synonymy.

DIAGNOSIS. Haplochromines with an adult size range of *ca* 96–145 mm SL, characterized by a number of dental and syncranial specializations.

The dentary has an almost square anterior outline, is very shallow over most of its length, is 'chinless' and has a marked lateral bullation of the area surrounding its bifurcation into ascending (coronoid) and horizontal arms. In the entire fish it has a very shovel-like appearance.

Premaxilla with very strongly inflated dentigerous arms, the broad alveolar surface extending almost to their posterior tips, and virtually circular in cross-section.

*Teeth in both jaws are arranged in broad bands (5–10 rows deep) of almost uniform width over their entire length; those of the outer row not separated by a distinct interspace from the inner rows, and, at least in fishes > 75 mm SL, continuing almost to the crown of the coronoid process (and often accompanied by one or more inner rows). Unicuspid teeth predominate in both the inner and outer rows of specimens in the known size range (*ca *55–145 mm SL),* but some bi- and tricuspid teeth occur amongst the inner rows in fishes < 100 mm SL.

DESCRIPTION

Habitus (Fig. 45). The straight or weakly concave, steeply sloping dorsal head profile, coupled with the broad, horizontal mouth and shallow, square-ended lower jaw give *Hoplotilapia* a very characteristic appearance. In other respects it is a typical, moderately deep-bodied haplochromine (depth of body 31–42% of SL, mean 38%).

The adult size range if from 96–145 mm SL.

Neurocranium. The skull has a moderately steep (50°–55°) and straight or very gently curved preorbital profile (see Greenwood, 1956*a*: fig. 8A; and 1974: fig. 76). Its preorbital depth is 34–35% of neurocranial length (*ie* deeper than the generalized type).

The supraoccipital crest is relatively high and expansive, with a near-pyramidical outline.

Dentition (See also Greenwood, 1956*a*: 322, fig. 8B; and 1974: fig. 74). In both jaws the outer row teeth are slender but strong, cylindrical in cross-section, strongly recurved, and with the crown but slightly, if at all, compressed.

Outer teeth in the lower jaw (Fig. 46) are implanted procumbently (the neck almost horizontal); those situated anteriorly in the upper jaw are effectively procumbent because the

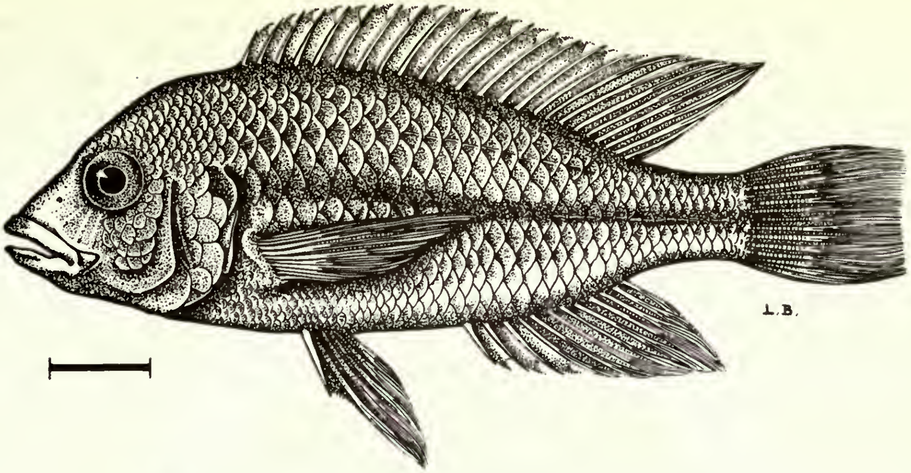

Fig. 45 *Hoplotilapia retrodens.* Lake Victoria. Scale = 2 cm.

premaxillary alveolar surface slopes forward and upward at an appreciable angle. Because of their strong recurvature, the crowns of the anterior teeth in the lower jaw are directed almost vertically, despite the near-horizontal alignment of their necks.

Most fishes >75 mm SL have the outer row of dentary teeth continuing onto the coronoid process of the bone, and ending near the coronoid crest (see below).

Unicuspid teeth predominate in the outer row of most specimens in the size range available for study (*ie* 55–144 mm SL), but a few lateral and posterolateral teeth may show faint traces of a minor cusp.

There are 40–68 teeth in the outer premaxillary row.

Unicuspid teeth also predominate in the inner tooth rows, with some bi- and tricuspid teeth present, especially in smaller fishes.

This predominance of unicuspid teeth in fishes < 90 mm SL can be considered a derived characteristic.

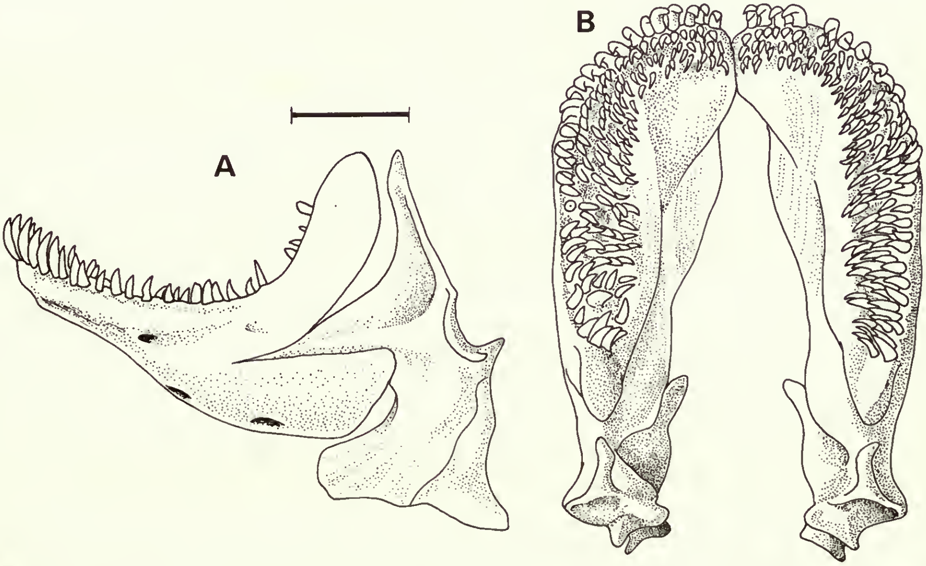

Fig. 46 Lower jaw of *Hoplotilapia retrodens* in: A. Lateral view, and B. occlusal view. Scale = 3 mm.

The most outstanding dental feature in *Hoplotilapia* is the great and almost uniform breadth of the tooth bands over the entire length of the dentigerous surface in both jaws (Figs 46 & 47). It will be recalled that the outer row of teeth in the lower jaw usually extends to near the apex of the coronoid process; the inner rows (here somewhat reduced in width) also extend onto the coronoid process, but stop short of the outer row by a distance of two or three outer teeth.

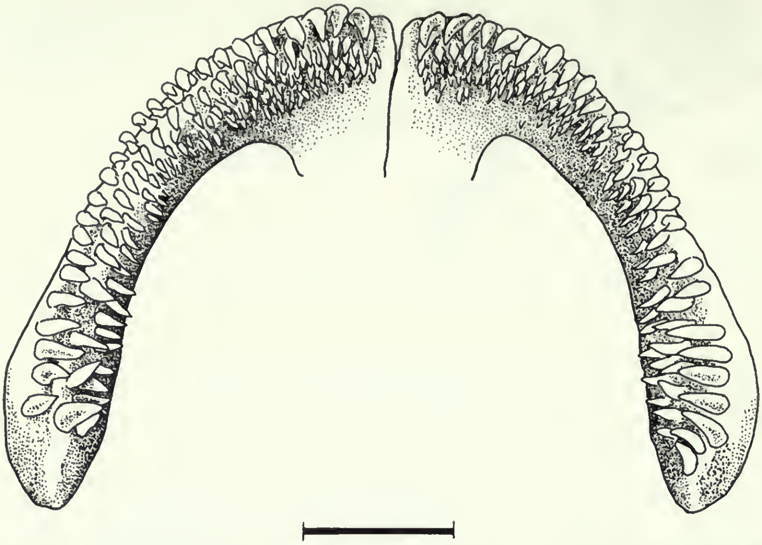

Fig. 47 Dentigerous surface of the premaxilla in *Hoplotilapia retrodens*, to show dental pattern. Scale = 3 mm.

Teeth forming the inner rows are not particularly close set, but are inserted across the entire width of the alveolar surfaces involved. There are 5–8 rows of teeth anteriorly, and 4–5 rows posteriorly on the premaxilla, with 5–10 anteriorly and 3–5 posteriorly on the dentary (see also Greenwood, 1956*a*: 322).

Upper jaw. The premaxilla is a robust bone with very strongly inflated dentigerous arms that are virtually cylindrical in cross-section, each widest over the posterior quarter of its length. The posterior fifth of each arm is bulbous (Fig. 47).

The ascending processes are much shorter than the dentigerous arms (half to two-thirds the length), and the articular processes are stout and anteroposteriorly expanded.

The maxilla is somewhat foreshortened and relatively deep, with a deeply concave medial face to its posterior arm (and a correspondingly bullate lateral face). Its articular head is strongly curved mediad.

Lower jaw. The dentary is a most distinctive bone, unlikely to be confused with the dentary in any other haplochromine from the Victoria–Edward–Kivu flock.

It is stout, with an almost vertical ascending (coronoid) arm which is, relative to the depth of the ramus, markedly elevated (Fig. 46A). This apparent shallowness of the dentigerous ramus is attributable to the way in which its lateral wall curves abruptly mediad from a level just below the alveolar surface. As a result of this curvature, the greater part of the ramus is almost horizontally (and not vertically) aligned and underlies the very broad alveolar surface (see Fig. 46B) beyond which it extends medially.

In lateral view the dentary is devoid of a 'chin', its anterior profile sloping steeply backwards and downwards. Whereas in other haplochromines the symphysial surface is either vertical or is inclined posteriorly, in *Hoplotilapia* it lies at an angle of *ca* 45° to the horizontal. The actual articular surface of the symphysis is relatively narrow in the vertical plane, but it is extensive in the near horizontal plane.

The region surrounding the dentary's bifurcation into ascending and horizontal arms is inflated, the lateral bullation emphasized by the shallowness of the ramus in that area.

About the anterior half of each ramus curves strongly mediad so that the anterior margin of the entire lower jaw is subrectangular when viewed dorsally.

The anguloarticular is deep and stout, the anterior margin of its anteroventral arm deep and rectangular in outline.

Lower jaw length is 34–41% of head length; the length/breadth ratio of the jaw varies intraspecifically from broader than long to 1·3 times longer than broad.

Lower pharyngeal bone and dentition. The bone is short and broad, its triangular dentigerous area equilateral in outline. All the teeth are cuspidate and relatively coarse, with those of the median rows stouter than the others (except for the posterior transverse row).

Contained species
Hoplotilapia retrodens Hilgendorf, 1888. Lake Victoria and, probably, the Victoria Nile; see Greenwood (1956*a*: 319–326).

DISCUSSION

Although many of the derived features characterizing *Hoplotilapia* are autapomorphies (eg. the gross morphology of the lower jaw, the form of the premaxilla, and the dental pattern in both jaws), most would seem to be foreshadowed in the *Ptyochromis* lineage, especially in *Ptyochromis xenognathus* and *P. annectens* (see pp. 62–65 above).

For example, in *Pytochromis* the tooth bands are broad in both jaws (but particularly in the dentary), there is a distinct tendency for the lateral wall of the dentary to curve sharply mediad, the teeth in the lower jaw are procumbent, the outer teeth in both jaws of larger specimens are strong but slender unicuspids and have markedly recurved crowns.

There are other resemblances too; for instance in overall neurocranial architecture, the robust lower jaw, the morphology of the anguloarticular bone, and the inflated dentigerous arms of the premaxilla. These could, however, be the products of convergence associated with the evolution of strong jaws since some or all of the features occur in *Neochromis* and *Lipochromis,* lineages that share no other derived characters with *Hoplotilapia* (see p. 52).

Those characters apart, the other synapomorphies do seem to suggest that *Hoplotilapia* may share a common ancestry with *Pytochromis,* and by an extension of that relationship, with *Paralabidochromis* and *Macropleurodus* as well (see pp. 66–67). This argument will be elaborated and evaluated when the possible relationships of *Hoplotilapia* and *Platyaeniodus* have been considered (see p. 80 below).

PLATYTAENIODUS Boulenger, 1906

TYPE SPECIES: *Platytaeniodus degeni* Blgr., 1906. Lake Victoria; see Greenwood (1956*a*: 312 & 315) for detailed synonymy.

DIAGNOSIS. Haplochromine fishes with an adult size range of *ca* 70–155 mm SL, readily diagnosed by their peculiar dental pattern.

Teeth in the dentary are grouped into two broad pyriform patches, contiguous anteriorly. In the premaxilla the teeth are arranged in a broad, inverted U-shaped band, whose arms and base are of almost uniform width in fishes < 100 mm SL, but in larger fishes the posterior parts of the arms are expanded medially so that they approach one another closely in the midline (Fig. 51). *There are corresponding modifications to the shape of the premaxilla and dentary, the latter having a near-circular outline when viewed occlusally* (Fig. 50).

DESCRIPTION

Habitus (Fig. 48). The gently curved, moderately steeply sloping dorsal head profile, coupled with the thickened, broad, beak-like projection of the premaxilla and the rounded anterior margin of the dentary, give to *Platytaeniodus* a most unusual physiognomy. This distinction is enhanced by the thickened lips (the lower often lying outside the upper lip), and by the almost completely hidden maxilla.

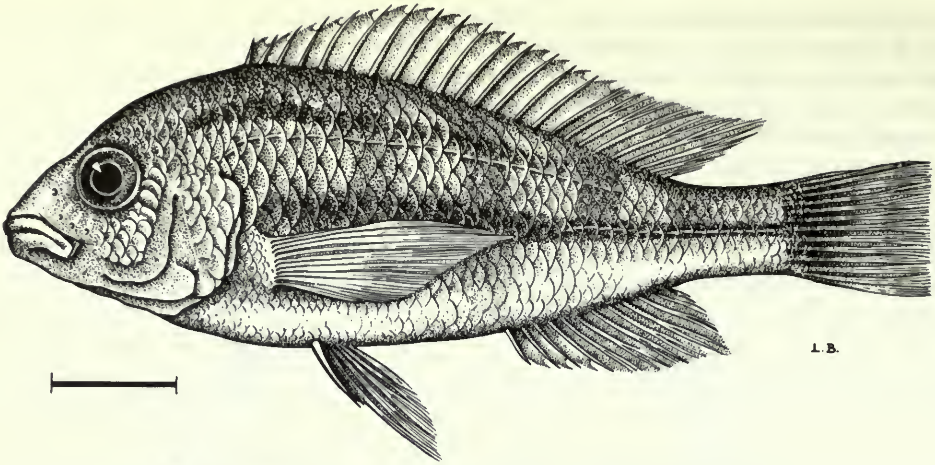

Fig. 48 *Platytaeniodus degeni.* Lake Victoria. Scale = 2 cm.

Adult size range is from 71–154 mm SL.

Neurocranium. Skull morphology in *Platytaeniodus* is close to that of *Paralabidochromis* (Fig. 49); that is, an anteriorly deepened variant of the generalized form (preorbital skull depth 36–37% of neurocranial length), with the preorbital region fairly strongly decurved and sloping at an angle of *ca* 55°–60° to the horizontal. The supraoccipital crest is moderately high, its outline near-pyramidical, and the anterior margin straight or gently curved.

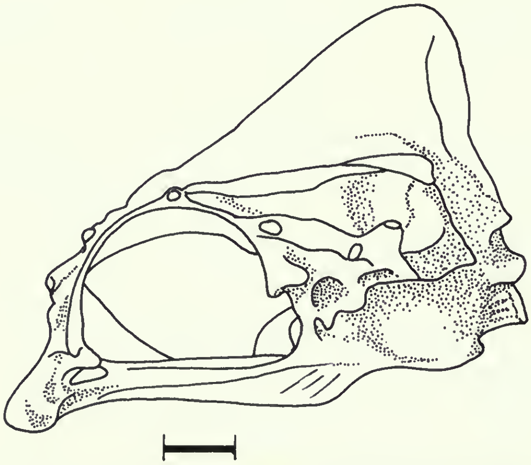

Fig. 49 Neurocranium (left lateral view) of *Platytaeniodus degeni.* Scale = 3 mm.

Dentition (See also Greenwood, 1956*a*: 312–3, 316 & fig. 6; 1974: fig. 73). The outer row teeth in both jaws are moderately slender but strong, are implanted vertically and are close-set. An admixture of uni- and unequally bicuspid teeth occurs in fishes of all sizes (smallest seen 67 mm SL), with unicuspids predominating in fishes > 90 mm SL. Unicuspid teeth have slender, conical crowns that are slightly broader than the near-cylindrical neck of the tooth; bicuspids have the crown a little compressed. In neither form is the crown strongly recurved; usually it is straight.

There are 36–50 teeth in the outer row of the premaxilla.

Inner teeth are either unicuspid or tricuspid, or there may be an admixture of both kinds with tricuspids predominating in fishes < 100 mm SL (particularly in the innermost rows).

There is a very gentle size-gradient between the outer row teeth and those of the inner rows. Virtually no interspace separates the two series. Like the outer teeth, those of the inner series are tall, slender and strong. Teeth in the innermost 2 or 3 rows are more compressed than the others. Implantation is vertical, and the crowns are slightly recurved.

It is in the arrangement of its jaw teeth that *Platytaeniodus* departs most markedly from the other lineages (Figs 50 & 51).

In both jaws the teeth are arranged in broad bands composed of 5–9 rows in the premaxilla and 5–7 in the dentary. There is no obvious anteroposterior decrease in the number of premaxillary rows but there is a size-correlated change in the dental pattern (Figs 50 & 51).

Small fishes (< 100 mm SL) have the bands either of uniform width over the entire length of the premaxillary alveolar surface, or there is a slight medial expansion of the rows on the posterior third of that surface (Fig. 50A). In larger fishes this medial expansion is continued

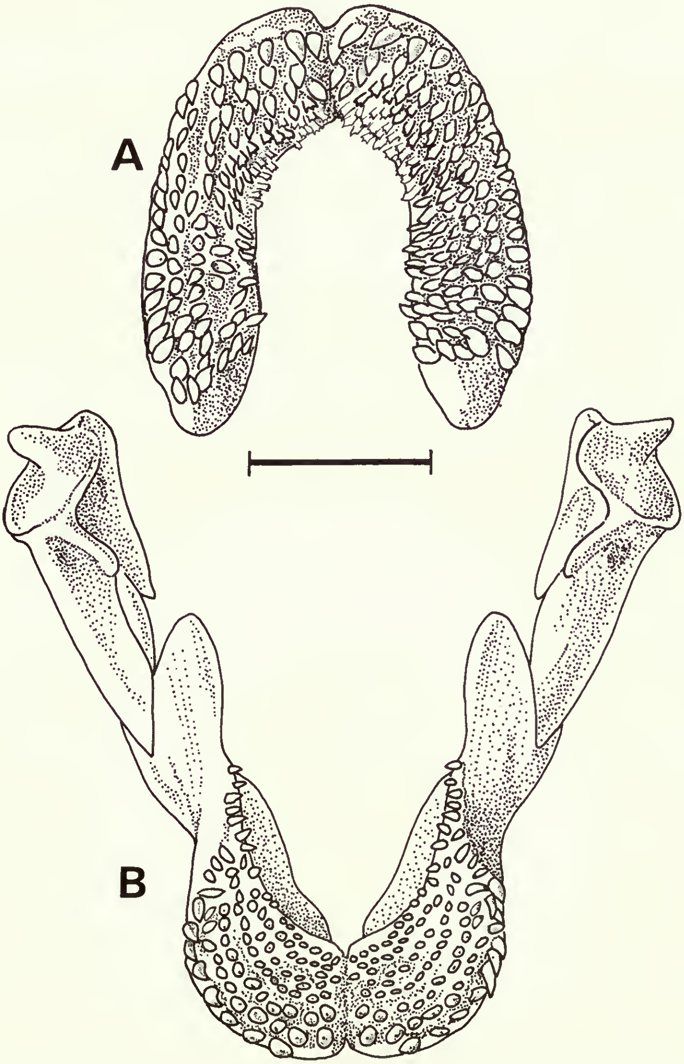

Fig. 50 *Platytaeniodus degeni*. A. Occlusal view of premaxillary dental surface. B. Lower jaw, in occlusal view.
From a small specimen (80 mm SL) to show dental pattern of premaxilla (**cf.** Fig. 51). Scale = 3 mm.

until, in fishes > 120 mm SL, the inner aspects of each arm are narrowly separated from one another (Fig. 51).

It should be stressed that this local expansion of the alveolar surface is not correlated with any increase in the number of tooth rows carried on it; these are always equal in number, or at most slightly fewer than those on the anterior and anterolateral regions of the bone.

Tooth bands on the lower jaw are less subject to variation in shape with body size. The teeth are confined to the anterior and anterolateral regions of the jaw, and are grouped into two broad patches roughly pyriform in outline and contiguous at the symphysis. Posteriorly on each side there is a short, single row of up to seven teeth lying between the main dental concentration and the base of the ascending arm of the dentary; these teeth are apparently a posterior extension of the outer tooth row.

Each pyriform patch is broadest anteriorly, narrowing rather abruptly over about its posterior sixth (Fig. 50B); before that point there is no decrease in the number of tooth rows.

The teeth in both jaws are so arranged that the tips of their crowns all lie in the same plane (and not, as is usual, with those of the outer row above the others).

As might be expected with a tooth pattern of this sort, the supporting bones, especially the dentary, are considerably modified even when compared with those in *Macropleurodus* and *Hoplotilapia.*

Mouth. The unusual, almost 'duck-billed' appearance of the mouth has already been noted. In most specimens the lower jaw is shorter than the upper, and laterally its well-developed, deep, lip usually lies outside the upper lip, hiding its lower margin posteriorly. The lips are not only thickened, but their free margins are also produced so as to extend above, or as in the case of the upper jaw, below the tips of the teeth.

Upper jaw. The maxilla is foreshortened and deep, with no appreciable mediad curvature of its articular head.

The premaxilla has its dentigerous arms gently inflated, even anterior to the origin of the ascending processes. Here the bone is drawn out into a narrow but deep, shelf-like expansion. The entire dentigerous part of the bone posterior to the shelf is virtually cylindrical in cross-section; it ends, on each side, as a short blunt projection formed

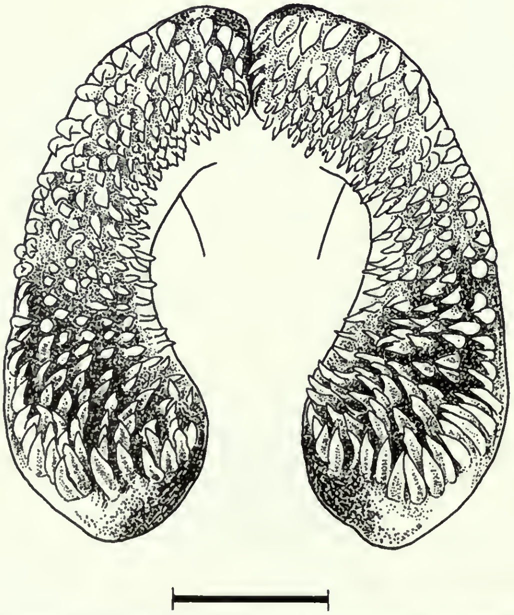

Fig. 51 *Platytaeniodus degeni.* Premaxillary dental surface (in occlusal view); from a specimen 120 mm SL. Scale = 3 mm.

immediately behind the last teeth (Fig. 51). Each arm of the bone has a marked downward curvature over almost the posterior third of its length (Fig. 52).

Both the ascending and the articular processes of the premaxilla are moderately stout; the length of the former is greater than that of the dentigerous arms.

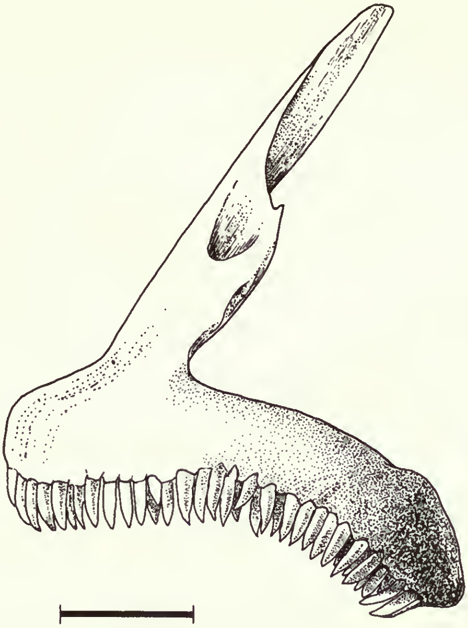

Fig. 52 *Platytaeniodus degeni.* Premaxilla in left lateral view; from a specimen 120 mm SL. Scale = 3 mm.

Lower jaw. In addition to being stout and foreshortened, the dentary has a most extraordinary overall apperance. Posteriorly, in the region of its division into ascending and horizontal arms, it is distinctly inflated, but the greatest departure from the generalized condition is seen anteriorly. The very broad and pyriform alveolar surface, and the bone supporting it, are produced outwards (almost to the ventral margin of the ramus) as an inflated, ovoid swelling. This projects laterally well beyond the rest of the bone (Fig. 50B). Below the swollen area, the ramus continues ventrally in almost the vertical plane; posteriorly, however, it curves sharply mediad, thus further emphasizing the swollen anterior region of the jaw.

As a result of this anterior swelling, the symphysial area on each ramus is both deep and wide anteroposteriorly, and the dentary has a very characteristic bulbous semicircular anterior outline.

The anguloarticular bone is deep and stout, the anterior margin of its anteroventral arm deep and subrectangular in outline.

Lower jaw length is from 32–40% of head length (mean 37%); the jaw is clearly longer than it is broad (1·2–1·7 times longer).

Lower pharyngeal bone and dentition. The bone is short and broad, its triangular dentigerous surface equilateral in outline. The teeth are coarse and cuspidate, those of the two median rows and the posterior transverse row stouter than the others.

Contained species

Platytaeniodus degeni Blgr., 1906. Lake Victoria; see Greenwood (1956*a*: 312–318).

DISCUSSION

Most of the derived features characterizing *Platytaeniodus* are autapomorphies (eg the peculiar dental pattern and shape of the lower jaw; the medial expansion of the premaxillary alveolar surfaces and the overall morphology of that bone). As such they give no indication of the taxon's interrelationships with other haplochromines in or outside the lakes under review.

Only the uniformly broad premaxillary tooth bands extending along the entire length of each premaxillary arm appear at first sight to be a synapomorphic feature shared with *Hoplotilapia* (see p. 74).

In other derived dental features, *Hoplotilapia* and *Platytaeniodus* have little in common, unless it be argued that fundamentally both taxa do have uniformly broad bands of teeth in the lower jaw as well. Those in *Hoplotilapia,* however, extend far onto the ascending process of the dentary, whereas in *Platytaeniodus* they are confined to the horizontal part of the bone, and have a very different arrangement anteriorly (**cf** Figs 46 & 50B). If the basic pattern is synapomorphic, then each taxon has departed from that basic condition along differently derived pathways.

Another possible synapomorphy lies in the nature of the dentary immediately below the anterior and anterolateral portions of its alveolar surface. In *Platytaeniodus* this region is hypertrophied to form the characteristically bulbous bow of the dentary. In *Hoplotilapia* this region of the dentary is inflated to form a deepened shelf of bone overhanging, laterally, the anteroventral aspects of the ramus; the shelf so formed resembles, albeit in an embryonic way, the peculiar stage-like development of the jaw in *Platytaeniodus.*

The sum of the various apparent synapomorphies shared by *Platytaeniodus* and *Hoplotilapia* would suggest that each taxon is the other's nearest living relative. That *Hoplotilapia* shows some synapomorphic similarities with, ultimately, the *Pytochromis* lineage, could indicate a shared common ancestry for that lineage (that is *Paralabidochromis, Macropleurodus, Hoplotilapia* and *Platytaeniodus*). The precise sequence of dichotomies interrelating the different taxa has, however, still to be resolved (see also p. 93).

MACROPLEURODUS Regan, 1922

TYPE SPECIES: *Haplochromis bicolor* Blgr., 1906 (type specimen only; see Greenwood, 1956*a*: 299–301). Lake Victoria.

DIAGNOSIS. Haplochromine fishes reaching a maximum adult size of *ca* 150 mm SL, usually with a very strongly decurved dorsal head profile (dorsum of snout sloping at *ca* 70°–80° to the horizontal), a small mouth and thickened lips, *the upper lip displaced laterally by the hypertrophied outer premaxillary teeth which, consequently, are exposed when the mouth is shut.*

Teeth in the outer row of both jaws are stout, with an inwardly directed, strongly recurved major cusp (lying at almost right angles to the neck) and a greatly reduced minor cusp (often merely a slight protruberance on the crown). The minor cusp is vertical and, because of the extreme curvature of the major cusp, lies labially to the tip of that cusp. Fishes > 80 mm SL have, laterally on the premaxilla, one or more inner tooth rows composed of enlarged teeth morphologically similar to those in the outer series.

DESCRIPTION

Habitus (Fig. 53). *Macropleurodus* has a very distinctive head and mouth, at least in specimens over 60 mm SL (smaller individuals are unknown). The dorsal head profile is generally very strongly decurved, the dorsum of the snout sloping steeply at an angle of 70°–80°; less commonly the profile is slightly curved (and may be straight). Annectant forms link the two extremes (see Greenwood, 1956*a*: 304–5, fig. 3).

The mouth appears to be relatively small, and has fairly well-developed lips. On one or both sides the upper lip is displaced dorsally by the hyperdeveloped lateral dentition. As a result, the teeth in that region are exposed, and the fish could be described as having a permanent leer on one or both sides of its face.

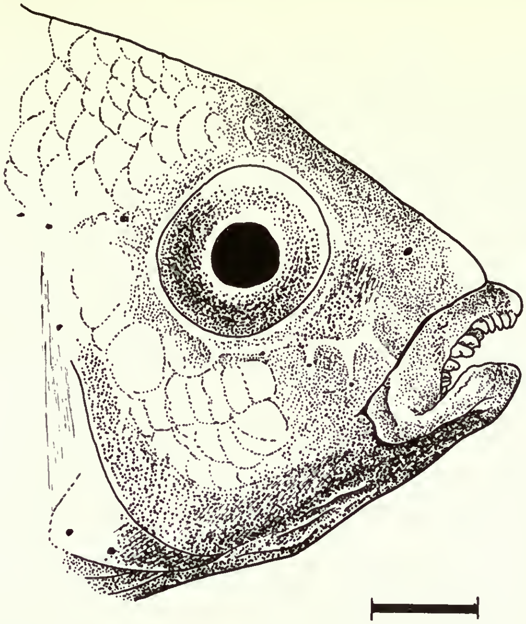

Fig. 53 Head of *Macropleurodus bicolor* to show naturally displaced upper lip and exposed dentition. Scale = 5 mm.

Adult size range for the only species, *M. bicolor,* is 80–150 mm SL; most specimens are sexually mature at lengths of between 90 and 100 mm.

Neurocranium. Despite some variation in the superficial dorsal outline of the head, the underlying preorbital profile of the skull is invariably steep and curved, the ethmovomerine region sloping at an angle of 80°–85°, its tip clearly reaching a level below that of the parasphenoid (Fig. 54; also Greenwood, 1956*a*: fig. 4A; and 1974: figs 66 & 76).

As would be expected in a skull of this shape, the preorbital depth of the neurocranium is high (34–37% of neurocranial length), particularly when compared with a generalized skull (24–30%, modal range 26–27%).

The supraoccipital crest is tall and expansive, with a near-pyramidical lateral profile.

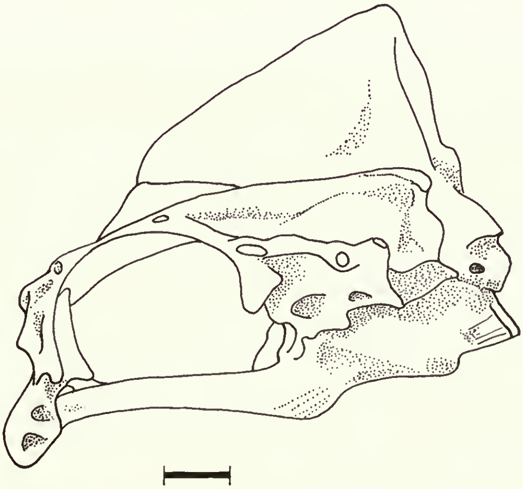

Fig. 54 Neurocranium (left lateral view) of *Macropleurodus bicolor.* Scale = 3 mm.

Dentition (see also Greenwood, 1956*a*: 299–301, and 304–5; 1974, fig. 75). The most derived features of *Macropleurodus* are to be found in its dentition, especially in the morphology of the upper jaw teeth and their arrangement on the premaxilla.

In both jaws, the outer teeth are stout, with a cylindrical to subcylindrical neck which merges gradually into a protracted, conical major cusp aligned almost at right angles to the neck.

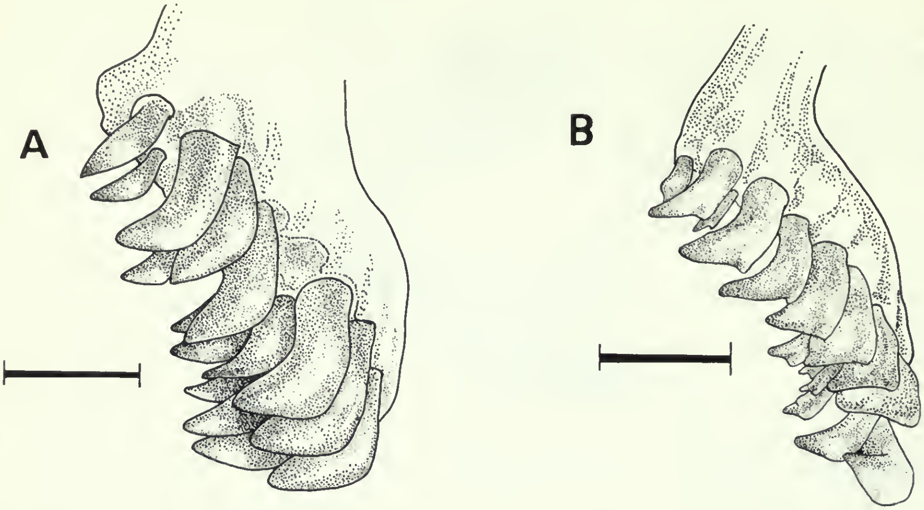

Fig. 55 *Macropleurodus bicolor.* Left premaxilla; the occlusal surface viewed medially and from somewhat below. A. Large fish (115 mm SL); the minor cusp is absent from all teeth; and B. Smaller individual (88 mm SL), to show the prominent minor cusp on all teeth (**cf.** Figs 43 & 57).

Superficially, the teeth in fishes > 100 mm SL appear to be unicuspid, but closer examination usually discloses a low bump on one side of the crown near the region of its juncture with the neck (Fig. 55A). In smaller fishes this swelling is discernible as a discrete, spur-like cusp inclined labially (Figs 55B & 57).

The major cusp is directed buccally, the arrangement of the teeth being such that in those situated laterally in the jaws, the crown lies at right angles to the anteroposterior axis of the row.

There is a clear-cut anteroposterior size gradient amongst the outer teeth, better marked in the lower than the upper jaw. Posteriorly in the lower jaw a few teeth barely show the characteristic morphology of the rostral elements in the row, and are little more than stout, incurved, uni- or weakly bicuspid teeth.

Anteriorly and anterolaterally, the outer dentary teeth are implanted somewhat procumbently, with the result that the morphologically 'outer' aspect of the crown forms a sloping occlusal surface. This unusual condition is emphasized because the line of tooth insertion dips distinctly ventrad over the anterior half of the dentary.

Premaxillary outer row teeth are, in contrast, vertically implanted; there are 24–40 (modally 34–36) teeth in this row.

Two kinds of inner teeth are present in the premaxilla, at least in fishes > 90 mm SL. Those in the first, or first and second inner rows, are stout, and in shape closely approximate to their counterparts in the outer row. Anterolaterally and laterally these teeth are larger than elsewhere in the row and are crowded together. Teeth forming the innermost row or rows of the series are weakly tricuspid (almost unicuspid) and small (but coarser than equivalent-sized tricuspids of the generalized type).

Such coarse, weakly tricuspid teeth are present in all the inner rows of fishes less than 90 mm SL.

There are 2–4 inner tooth rows anteriorly in the premaxilla, and 1 or 2 posterolaterally. Most of the specimens examined have the dextral tooth band a little wider than the sinistral one, and composed of slightly larger teeth. Symmetrical or sinistral hypertrophy has, however, been recorded.

A somewhat similar morphological differentiation is apparent amongst the inner teeth of the dentary. Here the outermost row is composed of relatively large, strongly recurved and uni- or bicuspid teeth that are both smaller and more refined than their counterparts of the outer row, but have essentially similar gross morphology. Teeth in the second and third rows are small, compressed tricuspids (occasionally bicuspids). The serial arrangement of inner row dentary teeth is regular, with 2 or 3 (sometimes 4) rows anteriorly and a single row posteriorly.

An infrequent variant of the basic tricuspid form in *Macropleurodus* is known. The lateral cusps are displaced behind and slightly medial to the central cusp, so that the tooth has a triangular crown with a cusp in each angle. Such teeth generally occur only in the outermost row of the inner premaxillary series.

What little information there is on the ontogeny of tooth form and pattern shows that buccal larvae (*ca* 9 mm total length) have slender, conical outer teeth indistinguishable from those in like-sized larvae of *Astatotilapia* (Greenwood: 1956*a*: 308). During later ontogenetic stages these teeth must be replaced by others having the characteristic *Macropleurodus* form and pattern. At a standard length of *ca* 85–95 mm it is known that certain lateral inner teeth on the premaxilla are replaced by enlarged teeth closely resembling their counterparts in the outer row.

Upper jaw. The dentigerous arms of the premaxilla are greatly inflated (especially anterolaterally), are cylindrical or nearly cylindrical in cross section, and have an expansive alveolar surface over the greater part of their length. This arm of the bone is distinctly arched at about its midpoint, the degree of curvature being greater on that side of the maxilla with the most enlarged teeth; see above (Greenwood, 1956*a*: fig. 4C).

The ascending premaxillary processes, as compared with the dentigerous arm, are slender and as long or longer than those arms.

The maxilla is foreshortened, its posterior portion relatively deep and with a pronounced median concavity (and thus a correspondingly strong bullation of the lateral face). Its articular head has a pronounced medial curvature.

Lower jaw (Fig. 56). The robust lower jaw (dentary + anguloarticular) is deep relative to its length, thus appearing foreshortened and massive.

Each ramus of the dentary is much inflated in the region surrounding its division into ascending and horizontal arms. Anteriorly the bone has a pronounced median curvature so that the entire jaw, viewed from above, has the outline of a broad-based U.

Anteriorly, the upper part of the dentary is greatly thickened, and has a broad superficial surface extending from the symphysis anteriorly to the base of the ascending arm posteriorly.

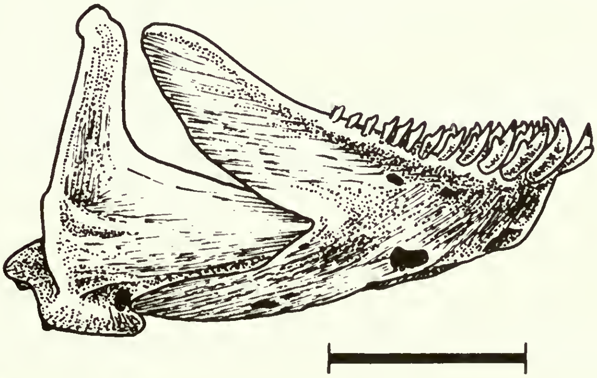

Fig. 56. *Macropleurodus bicolor.* Right dentary in lateral view. Scale = 3 mm.

Only about the outer half of this surface is dentigerous. Laterally, the ramus wall curves abruptly towards the midline so that it lies more nearly horizontally than vertically.

Each aspect of the symphysial surface is wide anterposteriorly, and runs almost vertically (**cf.** the backwardly sloping symphysis and resultant 'chinless' outline in *Paralabidochromis* p. 71).

The anguloarticular is massive and carries a broad and deep articular surface for the head of the quadrate. Its anteroventral prolongation has a near rectangular anterior margin and is so aligned that it runs downward in parallel with the posterior margin of the dentary (not ventral to that margin as it does in most other lineages).

Lower jaw length is from 28–36% of head length (mean 32%), that is somewhat shorter than in the generalized syncranium, but similar to that in most species of the *Paralabidochromis* and *Ptyochromis* lineages. Usually the lower jaw is as broad as it is long, but in some specimens it may be slightly longer than broad.

Lower pharyngeal bone and dentition. The relatively stout bone is short and broad, its triangular dentigerous surface broader than long. The teeth are cuspidate and compressed, but not noticeably fine; those in the two median series usually are coarser than the others (except those in the transverse posterior row).

Contained species

Macropleurodus bicolor (Blgr.), 1906. Lake Victoria; see Greenwood (1956*a* : 299–312)

DISCUSSION

Some of the derived features seen in *Macropleurodus* appear to be an intensification or elaboration of those found in *Paralabidochromis.* This is particularly apparent when the jaw skeletons and dentition of the two genera are compared. The skeletal modifications could, at least in part, be associated with the more massive teeth and expansive dental pattern characterizing *Macropleurodus.*

Neurocranial form in *Macropleurodus* also seems to represent a modification of the derivative trend manifest in the majority of *Paralabidochromis* species. Namely, an increase

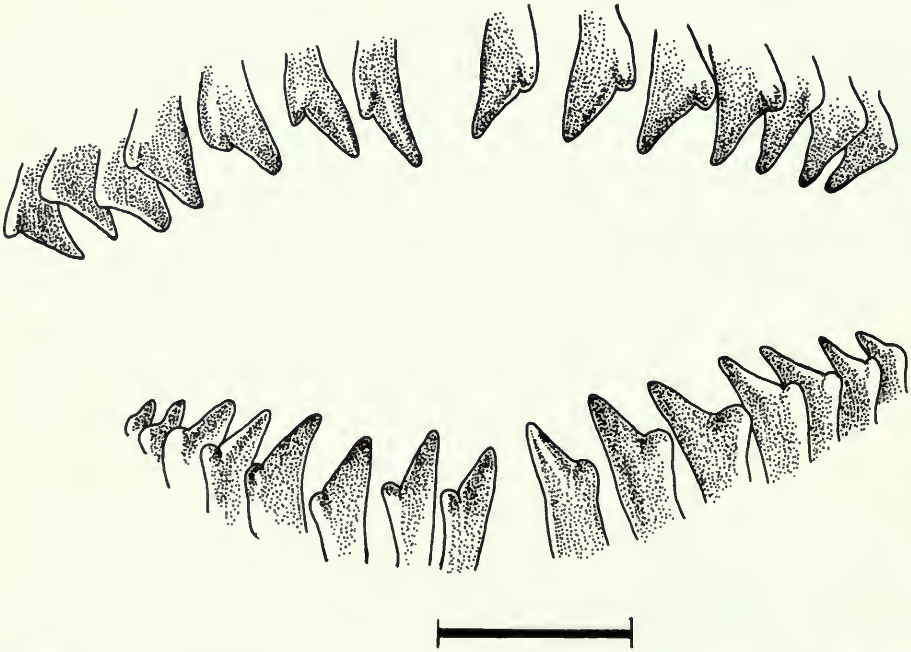

Fig. 57 Dentition of a juvenile *Macropleurodus bicolor*, viewed *in situ* and from in front, to show the nature of the crowns. Since the lips are not fully reflected, the bases of the teeth are not visible. (For comparison with Fig. 43.) Scale = 1 mm.

in the slope of the preorbital skull face, especially in the ethmovomerine region (**cf** the neurocranial descriptions for the two taxa, p. 81 and p. 68 respectively).

An apparently similar trend of apomorphic intensification could be invoked to explain the evolution of the peculiar outer tooth form in *Macropleurodus.* That is to say, from the unequally bicuspid teeth of a type seen in *P. beadlei* or *P. plagiodon,* the *Macropleurodus* type could develop by an increase in stoutness, the differential elongation of the major cusp, and an increase in its curvature towards the midline (**cf.** Figs 43 & 57). As noted before (p. 72), the outer teeth in small *Macropleurodus* do resemble those of adult *P. plagiodon.* It is also known that in *Macropleurodus* the peculiar inner teeth are developed relatively late in ontogeny, when the fish is between 85 and 95 mm long. Smaller individuals have inner teeth like those of comparable-sized, and larger, *Paralabidochromis.*

In the absence of other and more clear-cut synapomorphies it is possible to reach only a tentative conclusion about the relationships of *Macropleurodus*; namely, that *Macropleurodus* could share a fairly recent common ancestor with *Paralabidochromis.* The possible further relationships of *Paralabidochromis* are discussed on p. 93.

SCHUBOTZIA Boulenger, 1914

TYPE SPECIES: *Schubotzia eduardiana* Blgr., 1914. Lake Edward; for synonymy see Greenwood (1973 : 215–21).

Note. In my paper on the haplochromine species from Lake George (Greenwood, 1973), I placed this monotypic taxon in the genus *Haplochromis* (as then recognized), mainly on the grounds that '. . . To retain *Schubotzia eduardiana* in a separate and monotypic genus serves only to hide its close phyletic relationship with *Haplochromis*'. That sentiment was certainly valid when the genus *Haplochromis* had such a broad and non-monophyletic interpretation. However, the redefinition of *Haplochromis* (*sensu stricto*) and other elements of the old *Haplochromis* concept (Greenwood, 1979), negates my action and the reasons I gave for it. Following the methodology applied in the latter paper, this species must be given generic rank, and thus it returns to its former name, *Schubotzia.*

DIAGNOSIS. Small haplochromines (adult size range *ca* 55–80 mm SL), with a relatively shallow body (30–37% SL, mean 34%), thickened lips, a horizontal mouth in which the *lower jaw (29–35% head length, mean 33%) is shorter than the upper, and jaw teeth of a distinctive type.*

These teeth have an expanded crown that is markedly compressed and strongly recurved, and which constitutes almost half the length of the tooth; the overall appearance is one of a paddle with its blade bent at right angles to the shaft. Most teeth are unicuspid and the distal margin of the crown is rounded.

All outer teeth are moveably implanted and close-set, those of the dentary extending almost to the crest of the low ascending arm (coronoid) of the bone.

Inner teeth are small and tricuspid, *with strongly compressed and recurved crowns; virtually no interspace separates the outer row of teeth from the 2 or 3 inner series in the upper jaw, or the single (rarely double) series in the lower jaw.*

DESCRIPTION

Habitus (Fig. 58). The body is relatively slender (30–37% SL, mean 34%), the dorsal head profile straight or gently curved, sloping at an angle of 30°–35°. The thickened lips and the shorter lower jaw give the head a distinctive profile.

Neurocranium. Apart from its moderately decurved preorbital profile and more steeply sloping ethmovomerine region (which projects distinctly below the level of the parasphenoid), the skull is of a generalized type. Its preorbital depth is *ca* 30% of the neurocranial length, and the supraoccipital crest is low and wedge-shaped in outline.

Dentition. Outer teeth in both jaws have the crown greatly expanded relative to the slender subcylindrical neck and body, the much compressed crown constituting about half the height of the tooth (Fig. 59). Except for a few weakly bicuspid teeth in the smallest specimen

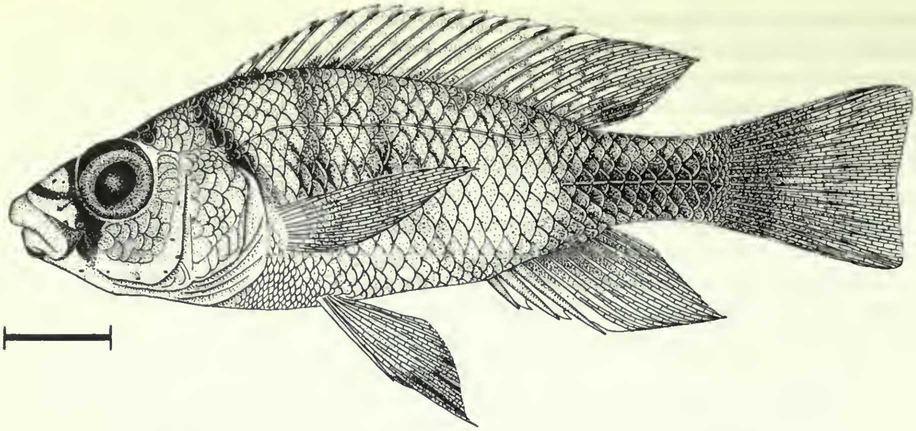

Fig. 58 *Schubotzia eduardiana.* Lake George. Scale = 1 cm.

examined (35 mm SL), the crown is unicuspid and its distal margin rounded. If the tooth were flattened out, it would have the shape of a paddle.

In bicuspid teeth, the minor cusp is not separated from the major one by a distinct gap, but merely by a narrow, V-shaped, groove.

The teeth are implanted vertically, but the strong buccal curvature of the crown results in that part of the tooth being aligned almost horizontally. In the lower jaw, the outer row is continued posteriorly almost to the tip of the low coronoid arm of the dentary. Rarely, a few small tricuspid teeth are intercalated, posteriorly, amongst the unicuspid outer teeth of the lower jaw. There is a slight anteroposterior size gradient in the height of the premaxillary teeth, and a more marked gradient in the lower jaw.

Both jaws have the teeth fairly close-set (but never with the crowns contiguous); in fresh material the teeth are moveably implanted.

There are 40–52 (mean 48) teeth in the outer premaxillary row. Teeth forming the inner rows are tricuspid and small, and have strongly compressed, recurved crowns. Almost no

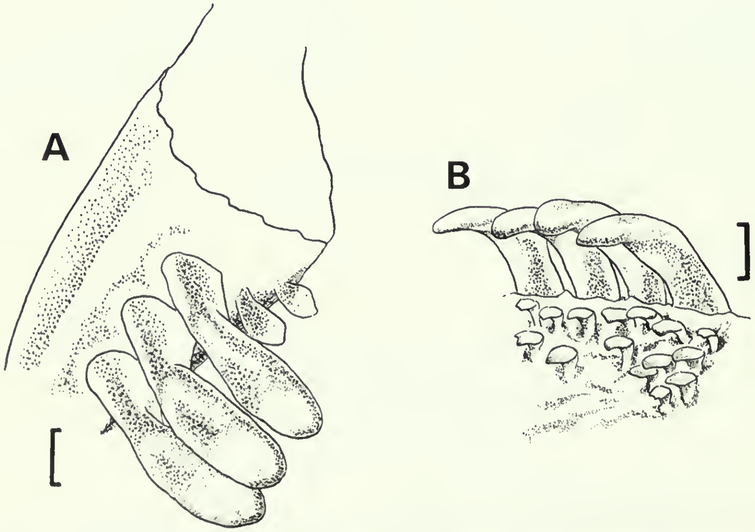

Fig. 59 *Schubotzia eduardiana.* A. Right premaxilla (in part), viewed medially and from below to show lateral aspect of the outer teeth. B. Teeth from the left dentary (anterolateral in position) viewed medially to show lingual aspect of the teeth. Scale = 0·25 mm.

space separates the outer teeth from those of the inner rows, of which there are 2 (rarely) or 3 in the upper jaw and a single (rarely double) row in the lower jaw.

Upper jaw. The maxilla is moderately foreshortened and deep; its articular head curved gently mediad.

The premaxilla is inflated and almost cylindrical in cross-section; its ascending processes are almost half the length of the dentigerous arms which, when viewed from below, have a broadly rounded U-shaped outline.

Lower jaw. The dentary is stout, deep (especially posteriorly) and foreshortened in appearance, with a low ascending (coronoid) arm; it is not noticeably inflated in the region around its bifurcation into ascending and horizontal arms (Fig. 60). The alveolar surface, at least anteriorly and laterally, is somewhat broadened, the inflation extending a little below the alveolar surface as a shallow dorsal bullation of the ramus wall. This bullation, like the overlying alveolar surface, clearly slopes forward and downward from a point near the upward curve leading into the coronoid arm (onto the greater part of which the outer tooth row is continued posteriorly and upwards).

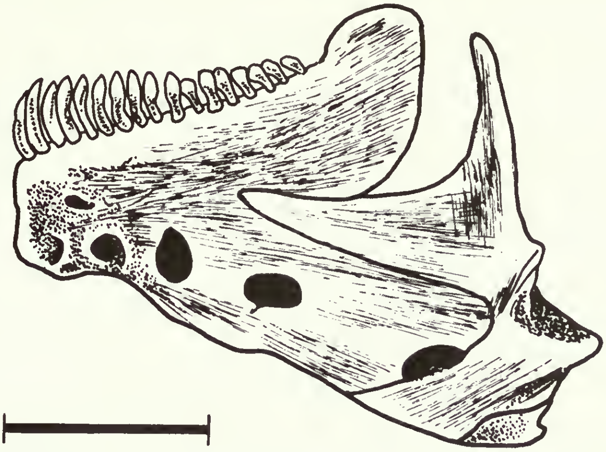

Fig. 60 *Schubotzia eduardiana.* Left ramus of lower jaw, seen from a somewhat ventrolateral position. Scale = 3 mm.

The anguloarticular is a little stouter than in the generalized type of jaw but, as in the latter, its anteroventral arm has an acute anterior angle; the arm itself lies almost horizontally beneath the posterior part of the dentary's ventral margin.

Length of the lower jaw is 29–35% (mean 33%) of head length; the length/breadth ratio of the jaw ranges from unity to 1·4 times longer than broad (mode 1·1 times).

Lower pharyngeal bone and teeth. The bone is relatively elongate and narrow; none of its teeth is enlarged (except, as usual, those in the transverse posterior row and, in larger fishes, a few posterior teeth in the median rows as well). The triangular dentigerous surface is about 1·3 times longer than it is broad.

Contained species

Schubotzia eduardiana Blgr., 1914. Lakes Edward and George; see Greenwood (1973 : 215–21).

DISCUSSION

Like the monotypic genera in Lake Victoria, *Schubotzia* is readily distinguished by its autapomorphic characters. But, it is extremely difficult to find its sister group amongst potentially related taxa because few of its derived features are shared ones.

The subalveolar bullation of the dentary in *Schubotzia* suggests a relationship with the Victoria lineages *Psammochromis* and *Allochromis* (see pp 55 & 59), as does the anteroventral slope to the outer tooth row on that bone; but, neither of the latter genera has the foreshortened and deep dentary of *Schubotzia*, and the actual dentition is distinctive in the three taxa (each being derived in its own way). The gross and detailed morphology of the dentary in *Schubotzia* also shares some features with that bone in the *Ptyochromis-Macropleurodus* assemblage, the possible sister group of *Psammochromis* and *Allochromis*. Thus there is a suggestion that *Schubotzia* is related to this lineage in its broadest sense, but it cannot be placed with certainty in either of the supposed sister divisions (see p. 94). On balance, the nature or degree of expression of its apparently synapomorphic features indicate closer relationship with the *Ptyochromis* assemblage.

Lake Victoria haplochromines of uncertain generic relationship

The status of the three species considered below will probably be resolved when studies on several newly discovered taxa are completed. Only one of the species treated here is represented by adequate study material, another factor hampering their full inclusion in the present revision.

'HAPLOCHROMIS' CRONUS Greenwood, 1959

When first described (Greenwood, 1959*b* : 180–2), and in a later publication (Greenwood, 1974), *'H' cronus* was thought to be a relative of species now placed in the nominate subgenus of *Lipochromis* (see p. 29 above). This assignment was based on the paedophagous habits of the few *cronus* specimens with food remains in the gut, and on some osteological features of the jaws. Superficially at least, and in its dentition, *cronus* appears to be more like the generalized species now placed in *Astatotilapia* (see p. 6) although it reaches a larger adult size (135 mm SL) than any member of that genus.

In one feature, an almost completely scaled caudal fin, *cronus* differs from all known haplochromines in the Victoria–Edward–Kivu assemblage; a completely scaled caudal is, indeed, generally considered to be the 'hall-mark' of haplochromines from Lake Malawi (see Regan, 1922 : 158). The value of this character as a phylogenetic marker, however, has still to be tested, and for the moment I shall disregard its presence in *cronus.*

Since the original description of *cronus* was prepared I have been able to examine one rather damaged and incomplete cranial skeleton, and thus gain more data on its osteological characteristics.

The morphology of the premaxilla and maxilla is very like that in members of the nominate subgenus of *Lipochromis,* as is the morphology of the lower jaw (dentary and anguloarticular bones), see p. 30. Other elements of the syncranium too are like those in *Lipochromis,* but all the resemblances involve either plesiomorph (*ie* non-derived) characters or those suspected of repeated and convergent origins.

The outer row jaw teeth in *cronus* are unlike those in either subgenus of *Lipochromis,* being large, relatively stout and caniniform unicuspids with recurved tips; none is embedded in the oral mucosa, which is not noticeably thickened.

In recently dead specimens the jaws are neither so markedly distensible nor so protractile as those in *Lipochromis,* even when compared with species of the nominate subgenus (see p. 30 above).

Thus, there are no clear-cut apomorphies shared by *cronus* and *Lipochromis*; the few apparent synapomorphies in jaw morphology also occur in lineages not thought to share a recent common ancestry with *Lipochromis* (see discussion on p. 52).

Dentally, '*H.*' *cronus* resembles members of the genus *Harpagochromis*, but its inclusion in that lineage is precluded by the morphology of its skull and jaws, features which, together with its large adult size, also exclude it from *Astatotilapia.*

Amongst the haplochromine material recently collected by members of the Leiden University research team there is at least one undescribed species which appears to resemble *cronus* both superficially and anatomically. When this taxon has been studied (especially in relation to other newly discovered paedophages) it may be possible to reconsider the status of '*H.*' *cronus.*

Until that time and until more material of '*H.*' *cronus* is available, little purpose would be served by giving the species any formal supraspecific grouping.

'HAPLOCHROMIS' APOGONOIDES Greenwood, 1967

I suggested originally (Greenwood, 1967 : 108), on the basis of its dentition and strongly decurved snout, that '*H.*' *apogonoides* could be related to species now placed in the genus *Ptyochromis* (see p. 60).

The dental resemblance, however, is actually confined to the morphology of the teeth (stout, very strongly recurved unicuspids), and does not include the dental pattern or other details.

In *apogonoides,* unlike *Ptyochromis,* the anterior outer teeth of the lower jaw are not implanted procumbently, there is no pronounced anteroventral dip in their line of insertion, there is a decided gap between the inner and outer series of both jaws, and the number of tooth rows anteriorly and anterolaterally is not increased above the generalized number (hence the tooth bands, compared with those in *Ptyochomis*, are narrower).

'*Haplochromis*' *apogonoides* also lacks the foreshortened and deep dentary and the stout, anteriorly obtuse ventral arm to the angulo-articular, derived features found in *Ptyochromis.* In fact the lower jaw of *apogonoides* is, in one respect, derived along the opposite morphocline from that manifest in *Ptyochromis.* It is, relatively speaking, longer than in the generalized type and much longer than that in *Ptyochromis* (45–51% of head length in *apogonoides,* **cf.** 22–38%, mode 35%, in *Ptyochromis*).

The two taxa do share certain apomorph jaw features (posteriorly bullate dentary, inflated dentigerous arms in the premaxilla) but, as noted for '*H.*' *cronus,* these are of doubtful validity when establishing interlineage relationships.

Thus there seem to be no grounds for assuming that '*H.*' *apogonoides* and *Ptyochromis* shared a recent common ancestor. Nor is it yet possible to find other characters indicating a close relationship of *apogonoides* with any other lineage in the Victoria–Edward–Kivu flock.

The extreme recurvature of the teeth in *apogonoides,* coupled with the morphology of its dentary, would seem to preclude any close relationship with *Astatotilapia, Harpagochromis, Gaurochromis* or *Lipochromis* (see pp. 7, 10, 32, & 27 respectively), some of whose species do have a superficial likeness to *apogonoides* (see Greenwood, 1967). Furthermore, *apogonoides* shares no apomorph features with any of these taxa, except perhaps with *Harpagochromis* an increased relative lower jaw length.

As with '*H.*' *cronus,* the situation may be clarified when certain newly discovered species have been studied more closely.

'HAPLOCHROMIS' THELIODON Greenwood, 1960

The few specimens of '*H.*' *theliodon* available for study (seven in all) are remarkably uniform in appearance (see Greenwood, 1960 : fig. 15) and all have two features which, when taken in combination, are very distinctive. Namely, a stout lower pharyngeal bone with numerous molariform teeth, and very small, deeply embedded scales on the thoracic region of the body. (The upper pharyngeal bones of the specimen prepared as an alizarin transparency are enlarged, but have only a few molariform teeth.)

The extent to which the lower pharyngeal bone and its dentition are hypertrophied is comparable with that in one species of *Labrochromis* (*L. humilior*) and that in *Gaurochromis* (*Mylacochromis*) *obtusidens*; the bone's outline is nearer that of *L. humilior.*

Rather surprisingly, the neurocranial apophysis for the upper pharyngeal bones in *theliodon* is not developed to a degree comparable with the apophysis in *L. humilior* or *Gaurochromis* (*M.*) *obtusidens.* It has only a slight expansion of the parasphenoid facet, and the basioccipital facets are no larger than those in the generalized type.

From both *L. humilior* and *G.* (*Mylacochromis*) *obtusidens, 'H.' theliodon* is immediately distinguished by the very small chest scales, a derived feature found in the lineage *Thoracochromis* (see Greenwood, 1979 : 290–5). In its hypertrophied pharyngeal mill, *theliodon* closely resembles *Thoracochromis pharyngalis* (Poll, 1939) of the Lake Edward drainage system. However, the small chest scales in *'H.' theliodon* do not have an abrupt size demarcation with the scales on the lateral and anterolateral aspects of the body (as is the case in all *Thoracochromis* species). Again, unlike *Thoracochromis,* there are more scales between the posterior part of the upper lateral line and the dorsal fin insertion (see Greenwood, 1979 : 291). Thus there are no grounds for placing *theliodon* in the *Thoracochromis* lineage, especially since it also lacks another *Thoracochromis* apomorphy, an incompletely scaled cheek.

Returning for the moment to those haplochromine lineages in Lake Victoria with which *'H.' theliodon* shares some derived features, *Labrochromis* and *Gaurochromis.*

The lower pharyngeal bone, as noted before, is like that in *Labrochromis humilior* but the apomorph chest scale pattern in *theliodon,* coupled with its lower, more streamlined skull, caution against supposing a sister-group relationship between these taxa on the basis of the pharyngeal mill alone. Also, an enlarged pharyngeal mill has evolved independently in lineages other than *Labrochromis* (eg in *Gaurochromis, Astatoreochromis* and *Thoracochromis*), and so its value as a phyletic marker in this context must be ranked rather low (see also p. 42).

The fine and numerous jaw teeth in all *Gaurochromis* are a derived feature (see p. 32), and are not shared with *'H.' theliodon.* An hypertrophied pharyngeal mill is also a derived feature but it is not possible to suggest that *theliodon* is the plesiomorph sister group to *Gaurochromis* on that basis because only one taxon in the *Gaurochromis* lineage has enlarged pharyngeal bones and teeth. The other species have fine pharyngeal bones and teeth, and since in other lineages this is the plesiomorph condition, it seems unlikely that the trend would be reversed in *Gaurochromis* (and that apart from the problems of convergence already noted).

Certain species of the genus *Psammochromis* do have small chest scales and a slight hypertrophy of the lower pharnygeal bone and dentition (see pp 54 & 56). But, all *Psammochromis* share derived features in the morphology of the lower jaw and its dental arrangement, (see p. 55). None of these features is present in *'H.' theliodon,* and the greater hypertrophy of its pharyngeal mill would also preclude it from plesiomorph sister-group status with *Psammochromis.* Likewise, since not all *Psammochromis* species have small chest scales, one cannot use that feature to suggest a close relationship with *'H.' theliodon.*

Similar arguments can be ranged against any attempted pairing of *'H.' theliodon* with other lineages from Lakes Victoria, Edward and Kivu. The species would, therefore, seem to be the sole representative of a distinct lineage and thus coordinate with those already accorded generic rank (see pp. 55 & 56). However, I hesitate to give *'H.' theliodon* that status until more specimens from a wider range of localities are available, and more is known of its syncranial anatomy.

Lake Kivu haplochromines of uncertain generic relationship

'HAPLOCHROMIS' SCHOUTEDENI Poll, 1932

This Lake Kivu species probably should be referred to *Paralabidochromis* (see p. 67), but I have not been able to see enough specimens, nor to obtain relevant osteological data, to reach a definite conclusion; see Poll (1932).

'HAPLOCHROMIS' WITTEI Poll, 1939

As with *'H.' schoutedeni,* a lack of material renders it difficult to place this Kivu species. Again, it would seem to be a member of the *Paralabidochromis* lineage.

Summary and conclusions

Some points of a general nature arising from this revision have been discussed in the introduction (p. 2), and others have been treated in an earlier paper (Greenwood, 1979 : 313–14). They need no repetition, except perhaps to reiterate that no progress has been made in resolving the problem of whether or not the Victoria–Edward–Kivu flock is of mono- or polyphyletic origin.

No unique apomorphy is shared by members of that flock and one cannot therefore erect a satisfactory hypothesis for its monophyletic origin. Equally, one cannot as yet find sister-groups outside the lake area for any of the endemic lineages described here. Thus, any hypothesized polphyletic origin is also without adequate foundations.

A lack of differentially shared apomorphies has also rendered it virtually impossible to establish sister-group relationships for lineages within the flock. Since, therefore, a complete and sequentially dichotomous cladogram for the flock as a whole cannot be established either, another line of evidence, in this case one indicating a monophyletic origin, is not available.

I say virtually impossible because some lineages do seem to be relatable on the basis of one, or at best a few, synapomorphic features. But, in these instances all that can be achieved is the formulation of the broad hypothesis '. . . These various lineages are more closely related to one another than to any other lineage (or group of lineages) because they alone share this (or these) synapomorph feature or features'. The 'others' still remain as phyletic isolates.

Again, within a lineage it has proved almost impossible to provide a precise and sequentially ordered series of dichotomies. A few dichotomies can be resolved at a high level of generality for the lineage (or group of related lineages) but beyond that one is usually left with the all too familiar unresolved tri- or polychotomy.

Brundin (1972) has laid great emphasis on the importance of the 'search for the sister-group' when constructing a cladistic phylogeny. In that respect my analysis of the Victoria–Edward–Kivu haplochromines has failed. The search for sister groups will have to be continued.

It cannot be argued, at the interlineage (*ie* intergeneric) level of universality, that the Victoria–Edward–Kivu flock is too young (at most 1my; see Greenwood, 1974) for the synapomorphies identifying sister groups to have evolved (see Brundin, 1972 : 110). The lineages exist and are presumed to be monophyletic on the basis of apomorphies unique to each. Any apparent synapomorphies developed in the future would not be true synapomorphies but convergences. Clearly, if synapomorphies exist they must be present now and are either indeterminable by the techniques applied to the problem, or I have failed to recognize them, or the sister-groups exist elsewhere.

Possibly the sister lineages may yet be identified outside the geographical area encompassing the Victoria–Edward–Kivu flock, for example amongst the '*Haplochromis*' species of Lake Malawi. They certainly cannot be recognized amongst the fluviatile haplochromines of east and central Africa (see Greenwood, 1979).

On the other hand, it has been suggested (Greenwood, 1974) that the Victoria–Edward–Kivu flock is but distantly related to that of Malawi. It would then have evolved from one or even several species more closely related to those now inhabiting the local river systems than to those associated with Lake Malawi. If that is the history of the two flocks, then I can foresee the greatest difficulties in ever constructing a fully sequential cladogram for the Victoria–Edward–Kivu flock.

The morphological equivalents of any hypothetical common ancestor (or ancestors) must be of an *Astatotilapia* type since none of the Victoria–Edward–Kivu taxa shows the derived features characterizing the other fluviatile lineages (see Greenwood, 1979). Because present-day *Astatotilapia* species cannot be sorted into sister species on the basis of anatomical synapomorphies, it is reasonable to suppose that the situation was no different in Pleistocene and pre-lake times. The synapomorphic features identifying a present-day lineage would,

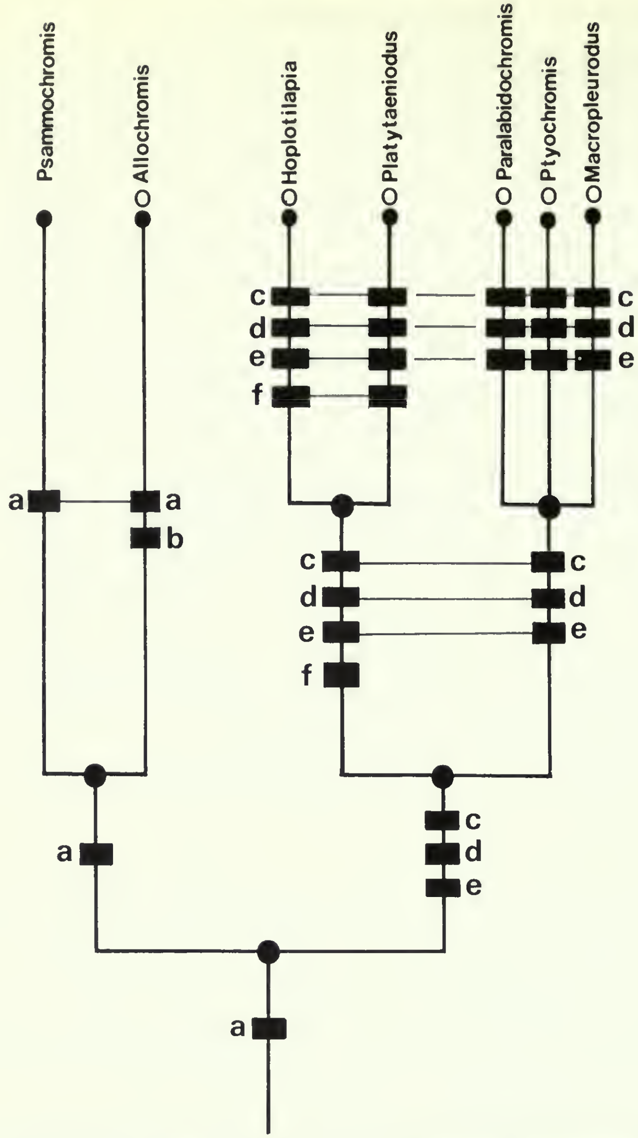
Psammochromis
O Allochromis
O Hoplotilapia
O Platytaeniodus
O Paralabidochromis
O Ptyochromis
O Macropleurodus
a
b
c
d
e
f

Fig. 61 Tentative cladogram for the *Psammochromis-Macropleurodus* super-lineage; see text pp. 93–94.

- ● Hypothetical common ancestor
- ○ Various autapomorphies (see text. pp. 57, 72, 75, 67, 62, & 80 for the taxa respectively).

a. Dentary slender, with a strong ventrad dip in the line of outer row tooth insertions anteriorly and anterolaterally, a marked lateral bullation of the ramus below that region.

b. Teeth in both jaws arranged in broad, crescentic bands over most but not all of the alveolar surfaces on the dentary and premaxilla.

c. Dentary foreshortened and deep, its lateral walls curving abruptly mediad a short distance below the alveolar surface of the bone.

d. Anterior outer row teeth of the dentary implanted procumbently (except in *Platytaeniodus*; see text p. 79).

e. Anterior margin to anteroventral limb of anguloarticular rectangular or bluntly rounded.

f. Teeth in broad bands on entire alveolar surface of the dentary and premaxilla.

therefore, be the apomorphic features evolved at the first (speciational) dichotomy leading to the origin of that lineage, and thereafter carried in it through successive speciation events. Under such circumstances it would be impossible to relate the two taxa resulting from that speciation event because the plesiomorph taxon would not show the diagnostic apomorph features of its derived sister species (and, subsequently, its descendent taxa as well).

Should the flock be of monophyletic origin, then a similar situation would exist if the plesiomorph daughter species of each dichotomy remained, in terms of derived features, indistinguishable from the mother species. In other words, one would have, through time, an anatomically identical line of stem taxa from which a series of primary side branches were split off. Each branch would be characterized by a different set of apomorph characters superimposed on the plesiomorph 'bauplan' common to every branch and to the successive stem species as well.

Clearly, if sister groups are to be identified, no matter how the Victoria–Edward–Kivu flock evolved, there is need for further and more detailed examination of the resultant taxa and, I would suspect, the use of characters other than strictly anatomical ones.

As mentioned earlier, some sister groups have been recognized amongst the lineages of that flock, with the result that two 'super-lineages' can be reconstructed.

The assemblage of species in the genera *Psammochromis, Allochromis, Paralabidochromis, Macropleurodus, Platytaeniodus* and *Hoplotilapia* (with possibly, *Schubotzia* as well) is the larger of the two super-lineages so far delimited (Fig. 61).

These, in many respects dentally diverse taxa are, with one exception, united on the basis of a single synapomorphy, the marked ventrad inclination, anteriorly and anterolaterally, of the outer tooth row in the dentary (see Fig. 61;a). The exceptional taxon, *Hoplotilapia,* has a very highly modified dentary, modified in such a way as to obscure the primary nature of its outer tooth implantation. *Hoplotilapia* is included in the group because of other synapomorphies which are shared with certain taxa having the group synapomorphy (see below).

The first dichotomy within this major assemblage (Fig. 61) is based on the nature of the overall morphology of the dentary.

In one of these primary divisions (*Psammochromis* and *Allochromis*) the dentary retains the slender, elongate facies of a kind not greatly different from the generalized condition, although it is somewhat inflated and bullate on either side of the symphysis. Dental pattern and tooth shape in *Psammochromis* and *Allochromis* are very different, with those of *Allochromis* showing a much derived condition, and those in *Psammochromis* retaining a more nearly generalized one (see pp. 54 & 59).

The other primary division (Fig. 61) is characterized by two, or possibly three, major synapomorphies. The first of these is shared by all members, namely a foreshortened, deep dentary, usually with the rami especially robust in that region occupied by the anterior bullation in *Psammochromis* and *Allochromis.* The second synapomorphy is shared by all but one genus (*Platytaeniodus*, see below) and involves the anterior dentary teeth being implanted procumbently (almost horizontally in two taxa). The third synapomorphy may be only a correlated character associated with the foreshortening, deepening and strengthening of the lower jaw; it concerns the shape and proportions of the anteroventral arm of the anguloarticular bone, which is deep and has a rectangular or rounded anterior margin (shallow and acute in the plesiomorph condition).

Other apparently derived features in the dentary involve the manner in which its lateral walls incline steeply, and in varying degrees abruptly, mediad, a condition foreshadowed in *Allochromis* of the other primary division (see above).

Hoplotilapia (see above) is included with the other taxa because of its deep, stout and foreshortened dentary, the shape of its anguloarticular, and because it has horizontally implanted dentary teeth which, in their derived gross morphology, resemble those in two other group members. *Platytaeniodus* (see above) is included, despite the vertical implantation of its teeth, because of the overall shape of its dentary and the anguloarticular.

Within this second primary division there are two further dichotomies, one of which terminates in an unresolved trichotomy (Fig. 61).

Members of one subdivision are characterized by having their oral teeth arranged in broad bands that extend over almost the entire dentigerous surface of both the premaxilla and the dentary. Its constituent taxa, both currently monotypic, are *Hoplotilapia* and *Platytaeniodus*; each is readily distinguished by various autapomorphic features.

Species belonging to the second subdivision (Fig. 61) are characterized by their teeth not occurring in broad bands over the entire dental surface of the jaws. In one genus (*Ptyochromis*) the inner tooth rows are wide anteriorly in the jaw, or even anteriorly and anterolaterally (*P. xenognathus*), but are reduced to a single row laterally and posterolaterally.

Three genera go to make up this subdivision, namely *Paralabidochromis, Ptyochromis* and *Macropleurodus.* Each is recognizable on the basis of its autapomorphies, but it is not possible to determine which two of the three taxa is the more closely related. Hence, the existence here of an unresolved trichotomy (Fig. 61).

Schubotzia, as was mentioned earlier, is a possible member of this super-lineage, but it typifies in many ways some of the difficulties encountered when one attempts to interrelate different lineages on a simple dichotomous basis.

The dentary in *Schubotzia* has a typical, downward sloping anterior deflection to the outer tooth row, thus suggesting that the fundamental relationships of the genus lie with the super-lineage. Its overall dentary form is nearest that in members of the *Ptyochromis-Paralabidochromis-Hoplotilapia-etc* primary division (Fig. 61) since it is relatively deep and foreshortened (not elongate and slender) although it does have the generalized type of anguloarticular seen in the *Psammochromis-Allochromis* primary division. The outer jaw teeth in *Schubotzia* have some autapomorphic features (see p. 85) but in their gross morphology (especially the broad spatulate crown strongly recurved on its fine and narrow neck) and in their vertical insertion on the dentary, these teeth closely resemble those of *Allochromis* and thus are of a shape not found elsewhere in the Victoria–Edward–Kivu flock. The dental pattern, however, is of a generalized type.

In brief, *Schubotzia* shares derived features with members in both the primary divisions of this super-lineage. It could be placed in one division or the other only if particular weight was given to a specific apomorphy (*ie* either the jaw shape or the tooth shape), and there are no grounds on which such an action could be based.

The problem created by *Schubotzia,* together with the uncertainties I entertain about the validity of the tooth-line character uniting the two primary divisions, are some of the reasons why I am treating this super-lineage as an informal assemblage of possibly doubtful phyletic significance. Likewise, in the current state of knowledge, I would hesitate to recognize formally the aggregated taxa in any of the three secondary dichotomies (*ie Psammochromis-Allochromis, Paralabidochromis-Ptyochromis-Macropleurodus,* and *Platytaeniodus-Hoplotilapia*).

A second super-lineage brings together four genera, *Enterochromis, Xystichromis, Neochromis* and *Haplochromis.* Here the sole apomorphy uniting the taxa is a long and much coiled intestine (all member species are phytophagous).

The primary dichotomy, based on dental apomorphies, results in one genus, *Enterochromis,* becoming the sister group of the other three genera combined.

Enterochromis retains an essentially underived dental morphotype and pattern, whereas its sister group shows various kinds of derived cusp form, and a trend towards an increase in the number of inner tooth rows with the resulting elimination of the gap between the inner and outer tooth series.

Within the tri-generic sister group, a secondary dichtotomy would separate *Xystichromis* as the plesiomorph sister taxon; the specializations seen in the dental morphology of *Haplochromis* and *Neochromis* are very disparate and thus for the moment it is probably best to consider the trio as an unresolved trichotomy.

Apart from the members of the two super-lineages discussed above, none of the other genera currently recognized can be interrelated. Consequently the general phylogenetic picture remains much as shown in the 'wheel diagram' used in my earlier analysis of the Victoria flock, in which, of course, the lineages were treated as subdivisions of a single genus (Greenwood, 1974).

The detailed picture, on the contrary, is different, with some groupings enlarged and others reduced as a result of redefined specific interrelationships, as well as the incorporation of species from lakes other than Victoria. Also, there would now be many more 'spokes' to the wheel, the result of a more critical assessment of the presumed apomorph or plesiomorph status of the characters (chiefly cranial ones) used to construct that provisional phylogeny.

A noticeable change involves the paedophagous species, which were considered to be a trophic group (or grade) of diphyletic origin (see Greenwood, 1974 : fig. 7, and discussions in the text). These species (with two exceptions, '*H.*' *cronus* [p. 88] and *Astatotilapia barbarae* [p. 32]) are now treated as a single phyletic lineage with two subdivisions (*ie* subgenera); see discussion, p. 31.

This arrangement, too, may come to be altered when a number of newly discovered paedophagous species from Lake Victoria has been studied in greater detail. Preliminary studies indicate that the present nominate subgenus (*Lipochromis*) may have to be given lineage (*ie* generic) status (and itself be subdivided). The phyletic integrity of the total lineage as now conceived, however, will be unaltered, and the paedophages will then become the third super-lineage.

More profound anatomical investigation of the two piscivorous lineages *Harpagochromis* and *Prognathochromis*, particulary the latter, may also lead to rearrangements within the genera and perhaps help to clarify their interrelationships with other members of the flock.

Naturally, any further research on the Victoria–Edward–Kivu flock will help towards clarifying relationships, but any equally important step in that direction must involve the haplochromines of Lake Malawi, if only to establish on more adequate grounds the suggestion that their relationship with the Victoria–Edward–Kivu assemblage is a distant one (Greenwood, 1974 : 99).

Almost 60 years ago, Regan (1922 : 160) concluded his revision of the Lake Victoria Cichlidae by writing '. . . it will be evident that I do not regard the classification here proposed as entirely satisfactory . . . at present I am not in a position to improve this arrangement'.

I can but appropriate his statement as an epilogue for my own work.

Acknowledgements

Since, in many respects this paper incorporates all my various '*Haplochromis*' studies, I can thank again all those people who helped me then, and many of whom have helped me again in the preparation of this paper.

In particular I am much indebted to my colleagues in the Fish Section of the British Museum (Natural History), Drs Ethelwynn Trewavas and Keith Banister, Margaret Clarke, Jim Chambers and Gordon Howes. They have contributed in so many ways; as audiences for my ideas, as critics, and as the source of ideas and information (not least in the difficult task of finding suitable names for the new taxa). To them all I proffer my warmest thanks. Especially is it a pleasure to thank Gordon Howes who has done so much for me, particularly in preparing most of the figures illustrating the paper (some taken from earlier work, others newly drawn) and in radiographing innumerable specimens (a job in which he was ably assisted by Margaret Clarke).

From amongst these many people I am, however, particularly beholden to Dr Ethelwynn Trewavas. She it was who introduced me to the fascinations of cichlid taxonomy some thirty years ago, and who has ever since been a source of inspiration and help (as she has been to so many other ichthyologists and fishery workers throughout the world). Thus, I would dedicate this paper to her on the occasion of her 80th birthday in November this year, with affection and gratitude.

A guide to the identification of haplochromine genera in Lakes Victoria, Kioga, Nabugabo, Edward, George and Kivu

Because few of the haplochromine genera from these lakes are recognizable on superficial characters alone, it is impossible to construct a simple key for their identification.

Instead, I have tried to produce a set of introductory pointers as a guide to generic identification using only features that can be ascertained readily. Any tentative identification made on this basis can then be checked against the relevant generic diagnoses, descriptions and figures. That step will be particularly important in those cases where the characters used in the guide are more applicable to groups of genera than to a single genus.

All haplochromines so far recorded from these lakes have a gradual size transition between the scales of the chest and those covering the ventral and ventrolateral aspects of the flanks; also, in all, adult males have true ocelli on the anal fin (see Greenwood, 1979 : 270, 281–2 and 274–6 for figures and discussions of these characters).

The five species treated as *incertae sedis* (pp 88–90) are not included in the guide.

Finally it must be emphasized that the guide is based on adult or near adult specimens because some of the characters utilized may not have reached their definitive expression in smaller fishes. The term 'adult size' refers to the size range of specimens which are either sexually mature or nearly so.

For a description of the various measurements used, see pp 4–6.

Anal fin with 4 or more spines . . . . ***Astatoreochromis*** (see Greenwood, 1979 : 285)

Anal fin with 3 spines . . . . A

A (i) Intestine at least 3–4 times standard length, and much coiled[1].
Fishes with a small adult size (80–105 mm SL). Usually the teeth fine, close-set and arranged in broad bands; in most taxa the inner series not separated from the outer row by a distinct gap B

(ii) Intestine less than 2½ times standard length and with few coils.
A wide range of adult sizes. Many different kinds of teeth represented amongst the numerous taxa, but generally the teeth are robust. Some taxa have the teeth in broad bands, but in most the inner teeth are in 2 or 3 series, and distinct from the outer row C

B (i) Outer teeth with a protracted and compressed major cusp, giving the crown an obliquely truncated appearance; the tip of the major cusp clearly lies beyond the neck of the tooth . . . . ***Haplochromis*** (p. 53) (see also, Greenwood, 1979 : 278–81)

(ii) *α*. Outer teeth unequally or subequally bicuspid, when unequally cuspid the major cusp clearly larger but not protracted; inner teeth in broad bands (4–6 rows). Dorsal head profile sometimes strongly decurved . . . . (a)

β. Outer teeth as above; inner teeth not in broad bands (1–3 rows); separated from the outer row by a distinct space. Outer teeth with the crown broader than the neck, close-spaced but not contiguous . . . . ***Enterochromis*** (p. 43)

(a) (*i*) Outer teeth unequally bicuspid, the crown not much, if at all wider than the neck; very close-set (often contiguous). Inner teeth in broad bands (usually 4–6 rows, sometimes up to 8) anteriorly and anterolaterally in the jaws, not obviously separated from the outer row by a distinct gap. Dorsal head profile not strongly decurved, usually straight . . ***Xystichromis*** (p. 46)

(*ii*) Outer teeth equally or almost equally bicuspid, close-set (usually contiguous); inner teeth in broad bands (usually 5 or 6 rows) anteriorly and anterolaterally, not separated from the outer row by a distinct gap. Dorsal head profile very strongly decurved. Mouth appears small . . . . ***Neochromis*** (p. 49)

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[1] If it is impossible to examine the gut, three of the four genera included under B can be recognized by their close-set, compressed, outer jaw teeth, which are moveably implanted, and by the rather wide bands of close-set inner teeth (generally not separated from the outer row by a distinct space). The fourth genus (*Enterochromis*) is not separable on dental characters from *Astatotilapia* (cf. full descriptions for other diagnostic features, especially the relative size of the nostril and the nasal lateral line canal opening).

C (i) Lower pharyngeal bone manifestly enlarged and stout, with more than the two median tooth rows composed of enlarged, molariform teeth . . . . ***Labrochromis*** (p. 37)
(see also **Gaurochromis (Mylacochromis)** (p. 36)

(ii) Lower pharyngeal bone not manifestly enlarged and stout (it may be slightly thickened), the median tooth rows not composed of molariform teeth, although often with slightly larger or coarser teeth (but these never have molariform crowns) . . . . . . D

D (i) Jaw teeth exposed, not buried in the oral mucosa, and of varied form in the different taxa. Mouth with varying degrees of protrusibility and distensibility but never very markedly distensible laterally and never with the anterior part of the lower jaw closing within the upper (Lower jaw may, however, be shorter than the upper). . . . . E

(ii) Jaw teeth small, deeply embedded in the oral mucosa, usually with only the tips of the outer teeth visible; in some species the tips of these teeth curve outwards. Inner teeth often completely hidden. Mouth large and protrusile, markedly distensible laterally. In some species the lower jaw is boat-shaped (narrow anteriorly), and its anterior part closes within the upper jaw; in others the lower jaw is broadly rounded anteriorly and does not close within the upper . . . . ***Lipochromis*** (p. 26)

E (i) Inner tooth rows in both jaws arranged anteriorly in 2 or 3 series (very exceptionally as many as 5 or 6), narrowing gradually to a single row posterolaterally; always separated from the outer row by a distinct gap . . . . F

(ii) Inner tooth rows in both jaws arranged in bands of equal or almost equal width over the entire dentigerous surface of the jaws, not separated from the outer row by a distinct gap.

(a) Inner tooth bands wide (5–10 rows), outer teeth neither enlarged nor stout . . (α)

(b) Inner tooth bands narrow (2 or 3 rows), outer and some inner teeth enlarged and stout; crown of outer teeth with a minute minor cusp and a strongly recurved and inwardly directed major cusp . . . . (β)

(α) (*i*) In both jaws the inner tooth bands (5–10 rows) are in the form of a broad-based U (outer and some inner rows in lower jaw usually continued onto the ascending process of dentary) Teeth unicuspid even in specimens < 70 mm SL. Lower jaw flat and shovel-like, its anterior margin rectangular . . . . ***Hoplotilapia*** (p. 72)

(*ii*) Wide tooth bands (6–10 rows) in the upper jaw either in the shape of a broad-based U (*ie* in fishes < 100 mm SL) or, in larger fishes, also U-shaped but with the posterior part of each arm greatly expanded medially so as almost to touch in the midline. Tooth bands of the lower jaw in the shape of two pyriform patches, contiguous medially. Anterior region of lower jaw rounded and bullate . . . . ***Platytaeniodus*** (p. 75)

(*iii*) Wide tooth bands (6–11 rows) in both jaws in the form of broad crescents which abruptly taper posteriorly, a single row (the outer) continuing for a short distance beyond the crescent. The bicuspid teeth in the outer row have the crown markedly expanded and much broader than the slender neck. Body slender (30–33% of SL), and elongate ***Allochromis*** (p. 57)

(β) Outer row of jaw teeth (and usually the first inner row) composed of stout bicuspids in which the minor cusp is greatly reduced and lies labially to the strong, elongate and bucally orientated major cusp; major cusp lying almost at right angles to the body of the tooth. Laterally on one or both sides the upper lip is reflected to expose the teeth, even when the jaws are closed . . . . ***Macropleurodus*** (p. 80)

F (i) Outer row of jaw teeth simple bi- and/or unicuspids (sometimes a few tricuspids as well); all inner row teeth smaller than those of the outer rows, and tri- and unicuspid . . G

(ii) Outer row jaw teeth with a long, markedly expanded and compressed, spatulate crown that is about half the length of the tooth (which is thus paddle-shaped in outline) and is strongly recurved (almost at right angles). In the lower jaw the outer row teeth extend onto the ascending arm of the dentary. Lower jaw shorter than the upper . . ***Schubotzia*** (p. 85)

G (i) Dorsal profile of head sharply concave; dorsal surface of snout almost horizontal; lower jaw sloping obliquely upwards at a marked angle (50–70° to the horizontal); cephalic portions of the epaxial musculature prominent. Head and body relatively compressed. Maximum adult length 117 mm . . . . . ***Pyxichromis*** (p. 24)

(ii) Dorsal head profile and overall head shape otherwise than in G (i); when mouth is oblique, the snout profile always slopes downwards and forwards (*ie* never horizontal or almost horizontal). When the dorsal profile is concave, the concavity is a gentle one . . . H

H (i) Body form slender and elongate (body depth 23–30% of SL, modal range 27–29%). Posterior $\frac{1}{4}$–$\frac{1}{3}$

of the premaxilla edentulous. A small maximum adult size (85–110 mm SL) **Yssichromis** (p. 22) also **cf. *Prognathochromis*** (p. 14)

Body form other than H (i); save for exceptional individuals, the body is deeper (30% (rarely)–47% of SL). Premaxilla fully toothed (edentulous posteriorly in some *Lipochromis* for which see back, D (ii)). Wide range of maximum adult sizes (from 50–230 mm SL). . . . I

I (i) Outer jaw teeth in both jaws slender, with strongly recurved crowns; 26–56 (usually 40–44) teeth in the outer row of the premaxilla. Inner teeth, also strongly recurved, arranged in broad bands (3–9 rows) anteriorly and anterolaterally in the jaws, narrowing to a single or double row laterally; separated from outer teeth by a distinct space. Lips usually thickened but not lobate. Lower jaw length 22–38% of head length (modal range 34–35%); lower jaw usually shorter than the upper. Dorsal head profile straight and steeply sloping (gently sloping in one species), or strongly decurved . . . . ***Ptyochromis*** (p. 60)

(ii) Outer jaw teeth strong but slender, moderately recurved; those situated anteriorly in the lower jaw inserted somewhat procumbently so as to form with the upper teeth a forceps-like bite. Rather few teeth in the outer premaxillary row (16–48, modal range 30–35). Inner teeth not arranged in broad bands. Lips thickened, lobate in one species. Dorsal head profile straight and sloping steeply . . . . ***Paralabidochromis*** (p. 67)

(iii) Dental patterns and gross morphology of the teeth, taken in combination, not as in I (i) & (ii) above: the genera, *Gaurochromis, Harpagochromis, Prognathochromis, Astatotilapia* and *Psammochromis.*

These genera are defined, principally, on osteological features. For their identification reference must be made to the full descriptions. As a rough guide, the following comments may be useful.

Gaurochromis (p. 32), has short, fine, compressed and close-set outer teeth, and in all but one species, a narrow, elongate lower pharyngeal bone with fine teeth. The exceptional species has a moderately enlarged lower pharyngeal bone with some molariform teeth; it is easily confused with *Labrochromis* (see p. 37).

Harpagochromis (p. 10) species reach a large maximum adult size (>200 mm SL) and have large jaws; there is, however, a strong superficial resemblance to *Astatotilapia*, especially in small specimens.

Prognathochromis (p. 14) species also have large jaws, but are more streamlined and shallower-bodied than species of *Harpagochromis*; they have what is generally thought of as a 'typical' predatory facies. There is a wide range of maximum adult body sizes, some species exceeding 220 mm SL, while others reach only *ca* 100 mm SL.

Astatotilapia (p. 6) species have a very generalized anatomy, pharyngeal and oral dentition, and few outstanding features in their gross appearance. The maximum adult size range is between *ca* 70–100 mm SL.

Psammochromis (p. 53) species, in their gross appearance, are intermediate between the slender-bodied, streamlined, *Prognathochromis* and the deeper, stouter-bodied *Astatotilapia* species. The lips are thickened (lower lip lobate in one species), and in some species the lower pharyngeal bone is slightly hypertrophied (with some enlarged, submolariform teeth).

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Index

Certain Victoria–Edward–Kivu species which are essentially fluviatile in habitat, but which do occur in the lakes, are dealt with in Greenwood (1979). They are listed here but marked with an asterisk, as are the lacustrine species dealt with in that paper.

Former binomen	Current generic placement	Page
*Astatoreochromis alluaudi**	*Astatoreochromis*	. .
Astatotilapia nigrescens	?*Prognathochromis*	20
Haplochromis acidens	*Psammochromis*	56
H. adolphifrederici	?*Labrochromis*	42
H. aelocephalus	*Psammochromis*	56
H. aeneocolor	*Astatotilapia*	8
H. altigenis	*Harpagochromis*	13
H. angustifrons	*Gaurochromis*	36
H. annectidens	*Haplochromis*	53
H. apogonoides	*Incertae sedis*	89
H. arcanus	*Prognathochromis*	19
H. argenteus	*Prognathochromis*	19
H. artaxerxes	*Harpagochromis*	13
H. astatodon	*Haplochromis*	53
H. barbarae	*Astatotilapia*	8
H. bartoni	*Prognathochromis*	19
H. bayoni	*Prognathochromis*	19
H. beadlei	*Paralabidochromis*	71
H. boops	*Harpagochromis*	13
H. brownae	*Astatotilapia*	8
H. cassius	*Psammochromis*	56
H. cavifrons	*Harpagochromis*	13
H. chilotes	*Paralabidochromis*	71
H. chlorochrous	*Prognathochromis*	21
H. chromogynos	*Paralabidochromis*	71
H. cinctus	*Enterochromis*	45
H. cinereus	*Astatotilapia*	8
H. crassilabris	*Paralabidochromis*	71
H. crocopeplus	*Prognathochromis*	21
H. cronus	*Incertae sedis*	88
H. cryptodon	*Lipochromis*	31
H. cryptogramma	*Prognathochromis*	21
H. decticostoma	*Prognathochromis*	19
H. dentex	*Prognathochromis*	19
H. dichrourus	*Prognathochromis*	19
H. diplotaenia	?*Harpagochromis*	13
H. dolichorhynchus	*Prognathochromis*	21
*H. dolorosus**	*Astatotilapia*	. .
H. eduardiana	*Schubotzia*	87
H. eduardi	*Astatotilapia*	8
H. elegans	*Astatotilapia*	8
H. empodisma	*Gaurochromis*	36
H. engyostoma	*Astatotilapia*	8
H. erythrocephalus	*Enterochromis*	45
H. estor	*Prognathochromis*	19
H. eutaenia	*Prognathochromis*	22
H. flavipinnis	*Prognathochromis*	20
H. fuscus	*Neochromis*	52
H. fusiformis	*Yssichromis*	24
H. gilberti	*Prognathochromis*	20
H. gowersi	*Prognathochromis*	20
H. granti	*Ptyochromis*	66
H. graueri	*Psammochromis*	56
H. guiarti	*Harpagochromis*	13
H. humilior	*Labrochromis*	42
H. ishmaeli	*Labrochromis*	42
H. labiatus	*Paralabidochromis*	71
H. lacrimosus	*Astatotilapia*	8
H. laparogramma	*Yssichromis*	24
H. latifasciatus	*Astatotilapia*	8
H. limax	*Haplochromis*	53
H. lividus	*Haplochromis*	53
H. longirostris	*Prognathochromis*	20
H. macrognathus	*Prognathochromis*	20
H. macrops	*Astatotilapia*	9
H. macropsoides	*Astatotilapia*	9
H. maculipinna	*Harpagochromis*	13
H. mandibularis	*Prognathochromis*	20
H. martini	*Astatotilapia*	9
H. maxillaris	*Lipochromis*	30
H. megalops	*Astatotilapia*	9
H. melanopterus	*Lipochromis*	31
H. melanopus	*Astatotilapia*	9
H. melichrous	*Prognathochromis*	21
H. mentatus	*Harpagochromis* (see *H. squamipinnis*)	13
H. mento	*Prognathochromis*	20
H. michaeli	*Harpagochromis*	13
H. microdon	*Lipochromis*	31
H. mylergates	*Labrochromis*	42
H. mylodon	*Labrochromis*	42
H. nanoserranus	*Prognathochromis*	20
H. nigricans	*Neochromis*	52
H. nigripinnis	*Enterochromis*	45
H. niloticus	*Xystichromis* (see *X. bayoni*)	48
*H. nubilus**	*Astatotilapia*	. .
H. nuchisquamulatus	*Xystichromis*	48
H. nyanzae	*Harpagochromis*	13
H. obesus	*Lipochromis*	31
H. obliquidens	*Haplochromis*	53
H. obtusidens	*Gaurochromis*	36
H. oregosoma	*Astatotilapia*	9
H. orthostoma	*Pyxichromis*	26
H. pachycephalus	*Harpagochromis*	13
H. pallidus	*Astatotilapia*	9
H. pappenheimi	*Yssichromis*	24
H. paraguiarti	*Prognathochromis*	20
H. paraplagiostoma	?*Harpagochromis*	14
H. paropius	*Enterochromis*	45
H. parorthostoma	*Pyxichromis*	26

H. parvidens	*Lipochromis*	31
H. paucidens	*Paralabidochromis*	71
H. pectoralis	*Harpagochromis*	31
H. pellegrini	*Prognathochromis*	20
H. percoides	*Prognathochromis*	20
H. pharyngomylus	*Labrochromis*	42
H. phytophagus	*Xystichromis*	48
H. piceatus	*Astatotilapia*	9
H. placodus	*Labrochromis*	42
H. plagiodon	*Paralabidochromis*	71
H. plagiostoma	*Harpagochromis*	13
H. plutonius	*Prognathochromis*	21
H. prodromus	*Ptyochromis* (see *P. annectens*)	66
H. prognathus	*Prognathochromis*	20
H. pseudopellegrini	*Prognathochromis*	20
H. ptistes	*Labrochromis*	42
H. riponianus	*Psammochromis*	56
H. sauvagei	*Ptyochromis*	66
H. saxicola	*Psammochromis*	56
H. schubotzi	*Psammochromis*	56
H. schubotziellus	*Astatotilapia*	9
H. schoutedeni	*Incertae sedis*	90
H. serranus	*Harpagochromis*	12
H. serridens	*Neochromis*	52
H. simpsoni	*Gaurochromis*	36
H. spekii	*Harpagochromis*	13
H. squamipinnis	*Harpagochromis*	13
H. squamulatus	*Harpagochromis* (see *H. pectoralis*)	13
H. sulphureus	*Prognathochromis*	21
H. taurinus	*Lipochromis*	30
H. teegelaari	*Labrochromis*	42
H. theliodon	*Incertae sedis*	89
H. thuragnathus	*Harpagochromis*	13
H. tridens	*Prognathochromis*	21
H. tyrianthinus	*Prognathochromis*	21
H. velifer	*Astatotilapia*	9
H. venator	*Prognathochromis*	20
H. vicarius	*Astatotilapia* (see *A. eduardi*)	8
H. victorianus	*Harpagochromis*	12
H. vittatus	*Prognathochromis*	20
H. welcommei	*Allochromis*	60
H. wittei	*Incertae sedis*	90
H. worthingtoni	?*Harpagochromis*	14
H. xenognathus	*Ptyochromis*	66
H. xenostoma	*Prognathochromis*	20
Hoplotilapia retrodens	*Hoplotilapia*	75
Macropleurodus bicolor	*Macropleurodus*	84
Paralabidochromis victoriae	*Paralabidochromis*	71
Platytaeniodus degeni	*Platytaeniodus*	79

British Museum (Natural History)
Associated publication on fishes

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A classification and the distribution of earthworms, suborder Lumbricina (Haplotaxida: Oligochaeta)

R. W. Sims

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A classification and the distribution of earthworms, suborder Lumbricina (Haplotaxida : Oligochaeta).

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Contents

Introduction 103
Classification 105
Systematic discussion 114
Distribution 116
Postscript and acknowledgement 122
References 122

Synopsis

Michaelsen (1921 & 1928) proposed a classification of earthworms based primarily on the structure and arrangement of genital systems. The classification gradually became a matter of controversy until eventually apart from megascolecoid species and members of the Lumbricidae, all other taxa were assigned to a heterogeneous Glossoscolecidae. Gates (1976*a*) recognized the systematic significance of common characters in the morphology of the ovaries and the process of shedding oocytes among members of the Lumbricidae and their undoubted allies which he employed to define the superfamily Lumbricoidea. These and other criteria are applied in a classification of the 16 families, 4 with 2 subfamilies, now forming the suborder Lumbricina with the recognition of five superfamilies. The present day distributions of the superfamilies are discussed in the context of palaeogeography: Criodriloidea and Lumbricoidea (Euramerica), Biwadriloidea (Pacifica, eastern Gondwana), Glossoscolecoidea (western Gondwana), Megascolecoidea (Gondwana).

Introduction

A biological classification is not static; it is transitory since a present day fauna represents a cross-section of evolutionary time and differs from both its antecedents and its descendents (Manton, 1977). Although aspects of this view of a classification are challengeable, the primary thesis is particularly apposite to those animal groups whose fossil histories are fragmentary or unknown. It introduces a dynamic concept into the formulation of affinities since, in many cases, change is inevitable but not solely because of animal evolution. Immediate reasons for modification are more likely to be due to a classification combining the totality of current knowledge of a group with contemporary zoological thought. Hence, frequent alteration is probable while new information and ideas continue to be advanced. Change was common during the nineteenth century as the numerous classifications proposed for the Oligochaeta provide testimony (Beddard, 1895). Beddard himself recognized three 'Groups': Aphaneura, Microdrili and Megadrili. The last, Megadrili, consisted of the true earthworms and their aquatic representatives and is equivalent to the suborder Lumbricina. Contemporary knowledge led Beddard to recognize only the following higher groups in his Megadrili : the single families Geoscolecidae (= Glossoscolecidae), Eudrilidae,

Bull. Br. Mus. nat. Hist. (Zool.) **39**(2): 103–124

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Lumbricidae and the superfamily Megascolecidae (sic) containing the families Perichaetidae, Cryptodrilidae and Acanthodrilidae of which the Perichaetidae contained perichaetine Megascolecidae *sensu* Gates (1959) and the last two comprised highly heterogeneous assemblages of megascolecoid genera. Since then many new taxa have been described and 16 families, four each with two subfamilies, are now recognized within the suborder (see below).

During the present century, the scientific contributions made by Professor Wilhelm Michaelsen between 1885 and 1938 have, justly, dominated oligochaetology and have fundamentally influenced its theory (Klatt, 1938). Michaelsen took the first steps towards constructing a comprehensive classification of the Oligochaeta in 1900 when he recognized new family groups some with subfamilies. The characters employed to delineate the basic units, the genera, and the families themselves were derived predominantly from the genital systems, especially the male terminalia. When he formally presented a structured classification in 1921 (modified slightly in 1928), it became clear that he did not regard these characters as markers (signifying a summation of other, somatic characters) but as being phylogenetically significant *per se*. Thus he engendered the belief that the genital systems are evolutionarily conservative while somatic characters are more liable to modification. This viewpoint subsequently had a profound influence on other authors, notably Stephenson (1930) and Yamaguchi (1953). Nevertheless Stephenson was uncertain about the higher systematics and dispensed with groups above the level of family in his great monograph.

Gradually information accumulated from intensive morphological studies, especially on the Lumbricina, and contributed towards a growing awareness that the 'classical' system of Michaelsen was no longer tenable and could not be regarded as inviolable. Moreover, against modern theories of speciation and evolution, many of Michaelsen's premises could be seen to be outmoded. A naivité of hypothesis was also widespread with most groups, genera or occasionally species, believed to be derived from extant groups; that is, ancestor and descendent were sympatric contemporaries. (Only infrequently were hypothetical common ancestors postulated to help explain present day relationships.) Generally there seemed to be a lack of awareness of knowledge derived from other animal groups, particularly those with rich fossil records. Consequently there was a failure to acknowledge that events in other groups could conceivably be paralleled in the Oligochaeta. Particularly the possibility that in the past more species and groups may have emerged and become extinct than survive to form the present day fauna. (A penetrating critique of the 'classical' system was presented by Gates (1972) in which he enumerated its many fallacies and others which have been derived from it.)

Most early difficulties were encountered in defining genera and consequently classifying them into families and the higher categories forming the suborder Lumbricina. The genera contained within the Megascolecoidea have always been accepted as forming a separate entity although apart from the Eudrilidae, there is still no general agreement on the number of families represented or the characters which should be employed to recognize them (Sims, 1966; Jamieson, 1971*b*). As for the non-megascolecoid genera, eventually they became to be assigned either as a series of families in a single superfamily (Yamguchi, 1953) or to the Lumbricidae *s.s.* (species with dorsal pores, pre-clitellar male pores, intestinal gizzards and lacking oesophageal gizzards) and all others to a highly structured Glossoscolecidae containing subfamilies and tribes (Jamieson, 1971*a*). Both treatments obscured the interrelationships of the included members and prevented a constructive discussion of the biogeography of the suborder. The problems encountered in accommodating new incontravertible lumbricoid genera led Gates to seek different criteria to obtain a new basis for a classification. Eventually he concluded that the morphology of the ovaries and the process of shedding oocytes provided attributes which could be employed to define the superfamily Lumbricoidea resulting in the formation of a seemingly homogeneous assemblage of families (Gates, 1976*a*).

Recently the debate on the classification of the Lumbricina was thrown open wider when Jamieson (1978) reported on a computer based investigation of the opisthoporous Oligochaeta. The principles of Hennig for deducing phylogeny were adapted for computer study and the attributes were analysed in an attempt to obtain a phylogenetic classification. As is often the case with taximetric studies, the results tended to reveal some evidence of primary categories but indications of secondary or lower categories were inconclusive. Nevertheless Jamieson proposed a classification of the Haplotaxida which apart from the inclusion of the Moniligastridae (accommodated in a separate suborder), is largely familiar but the compositions of the superfamilies forming the suborder Lumbricina although valid according to the methods employed, were seemingly artificial since their common characters were often adaptive (e.g. Almoidea = Almidae + Criodrilidae + Lutodrilidae); not surprisingly the distributional implications were incompatible with zoogeographical knowledge.

These problems however do not arise if the criteria recognized by Gates for defining the Lumbricoidea, the morphology of the ovaries and the budding of the oocytes, are applied together with other characters to all members of the Lumbricina. By utilizing these characters, superfamilies may be recognized which when polytypic, contain morphologically homogeneous assemblages which have common zoogeographical provenances. The ovarian characters recognized could be phylogenetically significant as they are seemingly non-adaptive, certainly it is difficult to suggest any selective agencies likely to have influenced their evolution.

Classification

The classification of the superfamilies proposed below is based on the ovarian characters first recognized by Gates (1976*a*) as useful for defining the Lumbricoidea. The structures regarded as systematically significant are seldom detailed by authors since they can be observed only by careful dissection in well-preserved material. During the preparation of this present work, it was impracticable to examine material representative of all of the 3000 or so species forming the Lumbricina, so only sample species were dissected. In these circumstances the classification can be no more than tentative and some characters may, in time, be found to be variable in their expression. However, when the validities of the component groups are not doubted, variation in a key character need not invalidate the classification; instead only the weighting and definition of the taxonomic criteria may need re-assessment and modification*.

Each family and, when recognized, subfamily is briefly defined to assist in identification. Many of the characters listed are not individually diagnostic but when present in varying combinations with other attributes, permit groups to be recognized. A few characters, some possibly of phylogenetic significance, are not included especially those derived from the vascular and excretory systems. These details are omitted due to the paucity of reliable information about their expressions in many species of the larger families.

Meanwhile parts of the classification are likely to remain controversial until the significance of a few characters has been more rigorously investigated or additional structures are recognized as being taxonomically important. For example, many components of the Megascolecoidea currently defy classification into groups which receive universal accep-

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*Gates (1968) described the genus and species *Thamnodriloides yunkeri* (family Glossoscolecidae, superfamily Glossoscolecoidea) on a single aberrant specimen with oocytes forming numerous egg-strings, a character diagnostic of the superfamily Megascolecoidea. Variation in this character has not been studied so the significance of the observation is unknown. However, in some Glossoscolecoidea, the ovaries tend not only to be lobate but occasionally have filaments which in preserved specimens may be interpreted as egg-strings. Gates (*personal communication*) warned of variations in the form of the ovary and disposition of the oocytes in preserved specimens, for example in species where the oocytes are normally shed individually, on preservation they may form clumps which can be interpreted as strings. Like other attributes, the characters of the ovaries and the oocytes should be assessed on their expressions in series of specimens and not in individuals. In the case of *Thamnodriloides yunkeri*, the report of an exception in a single, aberrant specimen should not cause the system to be rejected since other characters present permit the species to be classified (fan-shaped ovaries, subneural vessel free of the nerve cord, the presence of a supra-oesophageal blood vessel and extra-mural calciferous glands and the absence of prostatic glands associated with the male pores).

tance. In this case, a pragmatic solution is adopted which although not entirely incompatible with available information, provides working groups composed of morphological grades which may not necessarily be phylogenetic assemblages.

Key to the families of the suborder LUMBRICINA

1	Prostatic glands present (discharging through or near male pores or on segments adjacent to the male pores) or 'prostate'-like bursae discharging through male pores	2
	Prostatic glands absent ('prostate'-like glands, when present, not associated with the male pores)	9
2	Male pores anterior to or on segment *xvi*	3
	Male pores posterior to segment *xvi*	5
3	Male pores on segment *xiii* (lateral line present, aquatic, Japan)	**BIWADRILIDAE**
	Male pores on segments *xv* or *xvi* (lateral line absent)	4
4	Body quadrangular (male pores on porophores, aquatic Europe)	**CRIODRILIDAE**
	Body cylindrical (male pores in copulatory pouches, terrestrial Madagascar)	**KYNOTIDAE**
5(2)	Spermathecae present in pre-testicular segments	6
	Spermathecae absent from pre-testicular segments (received sperm contained in coelomic sacs associated or communicating with the ovisacs and oviducts) .	**EUDRILIDAE**
6	Prostatic glands racemose without central duct	**MEGASCOLECIDAE**
	Prostatic glands tubular with central duct	7
7	Meronephric	**OCTOCHAETIDAE**
	Holonephric	8
8	Last hearts or homoetic equivalent in segment *xi*	**OCNERODRILIDAE**
	Last hearts posterior to segment *xi*.	**ACANTHODRILIDAE**
9(1)	Oesophageal gizzard(s) or gizzard-like dilation(s) present in the pre-testicular segments	10
	Oesophageal gizzard(s) or gizzard-like dilation(s) absent from the pre-testicular segments	14
10	Extra-mural calciferous glands present	11
	Extra-mural calciferous glands absent	12
11	Gizzard in segment *vi* (supra-oesophageal blood vessel present)	**GLOSSOSCOLECIDAE**
	Gizzard in segment *vii* (supra-oesophageal blood vessel absent).	**MICROCHAETIDAE**
12(10)	Body quadrangular in cross-section, at least in the post-clitellar region (supra-oesophageal blood vessel present)	**ALMIDAE**
	Body cylindrical (supra-oesophageal blood vessel absent).	13
13	Male pores paired on segment *xv* (2 or 3 gizzards, each restricted to a single segment)	**HORMOGASTRIDAE**
	Male pores paired on segment *xxii* (1 gizzard restricted to a single segment, or, 2 gizzards each occupying two segments)	**AILOSCOLECIDAE**
14(9)	Testes 2 pairs in segments *x* and *xi* (intestinal gizzards, when present, in some or all of segments *xvii-xx*)	15

Testes 10 pairs in segments *xii-xxi* (intestinal dilation in segments *xxi-xxiv*) . . . . **LUTODRILIDAE**

15 Intestinal gizzards present (intra-mural calciferous glands present) . **LUMBRICIDAE**
Intestinal gizzards absent (calciferous glands absent) . **SPARGANOPHILIDAE**

Suborder **LUMBRICINA**

Earthworms and their aquatic representatives: clitellum formed from multiple layers of cells; testes usually 1 or 2 pairs in *x* and/or *xi* (exceptionally numerous: *Agastrodrilus,* family Octochaetidae, 9 pairs and *Lutodrilus,* family Lutodrilidae, 10 pairs) when there are 2 pairs of testes, the two vasa deferentia of each side usually unite; male pores 1 pair, rarely 2 pairs, at least two segments behind the posterior testes; ovaries commonly 1 pair in *xiii* (*xiv* and *xx* in *Agastrodrilus, xxiii* in *Lutodrilus*), oocytes small, not yolky; female pores in *xiv* (*xv* and *xxi* in *Agastrodrilus* and *xxiv* in *Lutodrilus*).

Distribution. World wide, except Antarctica.

Superfamily **CRIODRILOIDEA**

Fresh and brackish water worms: lateral line absent; ovaries small, flattened, pear to paddle-shaped, oocytes shed individually, not forming egg-strings; calciferous glands absent; supra-oesophageal vessel absent; subneural vessel adherent to the nerve cord; hearts lateral.
Single family.

Distribution. Southwestern palaearctic.

Family **CRIODRILIDAE** Vejdovsky, 1884.

Fresh and brackish water worms: body quadrangular in cross-section; dorsal pores absent; clitellum annular, extensive, indistinctly delimited anteriorly and posteriorly (*xiv, xv*) *xvi–xxxxv* (*xxxxvi*), tubercula pubertatis absent; male pores paired *xv* on porophores; spermathecal pores absent (tubular to hornshaped spermatophores usually present on the body wall near *xiii*); gizzard? rudimentary (oesophageal wall thickened *v–vii*), intestine thickened anteriorly *xv–xx* (*xxi*); paired hemispherical bursae or 'prostatic glands' *xv*; spermathecae absent; meganephridial.
Single genus with two(?) species.

Distribution. France, Germany, Italy, Yugoslavia, Hungary, Poland, southern U.S.S.R., Syria and Israel; introduced into the U.S.A. (plant pots, Baltimore).

Superfamily **LUMBRICOIDEA**

Earthworms some freshwater: lateral line absent exceptionally rudimentary (Sparganophilidae); ovaries small, discoidal with the oocytes forming a single egg-string; supra-oesophageal vessel absent; subneural vessel, when present, adherent to the nerve cord; hearts lateral.
Five families.

Distribution. Holarctic, some species introduced into other regions

Family **SPARGANOPHILIDAE** Michaelsen, 1928

Freshwater worms: body cylindrical but capable of forming a dorsal groove; lateral line doubtfully present; dorsal pores sometimes present anteriorly or absent throughout; clitellum saddle-shaped (*Sparganophilus tamesis* and *pearsei*) or annular (*S. smithi*), (*xiv*)

xv–xxv (*xxviii*), paired tubercula pubertatis present, usually ridge-like but may be divided intersegmentally to form a series of pads; male pores paired, inconspicuous, 18/19 or *xix*, intraclitellar; spermathecal pores paired or multiple, inconspicuous (5/6) 6/7/9; gizzards and calciferous glands absent; prostate-like glands present, *not* associated with the male pores, possibly up to 14 pairs but commonly 4 or less in *xxii–xxvi;* spermathecae one to four pairs per thecal segment, adiverticulate; meganephridial.
Single genus and 3 species.

Distribution. North and Central America (Ontario, Michigan, North Carolina, California, Guatemala, Mexico); introduced into Britain and France.

Family **AILOSCOLECIDAE** Bouché, 1969

(syn. Komarekionidae Gates, 1974)*

Earthworms: body cylindrical, dorsal pores absent; clitellum partly annular (*Ailscolex*), otherwise saddle-shaped, *xiv–xxiv*; tubercula pubertatis paired as continuous bands throughout most of the saddle-shaped region of the clitellum; male pores paired, inconspicuous *xxii*; spermathecal pores 6/7/8/9 (*Komarekiona*) and 8/9/10 (*Ailoscolex*); oesophageal gizzard(s) present, single in *vi* (*Komarekiona*) or 2 gizzards the first in *vi, vii* and the second in *viii, ix* (*Ailoscolex*), intestinal gizzards absent; calciferous glands absent; tubular, prostate-like glands associated with the tubercula pubertatis and (*Komarekiona*) additionally associated with the ventral setae in some segments *vii–xxvi*; spermathecae adiverticulate; meganephridial.
Two monotypic genera.

Distribution. *Ailoscolex* southwestern France (central Pyrenees); *Komarekiona* southeastern United States (North Carolina, Tennessee and Indiana).

Family **HORMOGASTRIDAE** Michaelsen, 1900.

Earthworms: usually large, body cylindrical; dorsal pores absent; lateral setae more closely paired than ventral setae; clitellum saddle-shaped (*xiii*) *xiv–xxiv* (*xxxii*), tubercula pubertatis paired, ridge-like (*xxvii*) *xix–xxiv* (*xxix*); male pores *xv* by 15/16, preclitellar; spermathecal pores inconspicuous, paired or multiple 9/10/11/12/13/14/(15); 2 or 3 oesophageal gizzards *vi–viii*; single intestinal gizzard rudimentary *xv, xvi* (*xviii*); calciferous glands ?absent, prostatic glands absent; spermathecae adivertculate; meganephridial.
Two doubtfully distinct subfamilies.

Distribution. Western Mediterranean countries.

Subfamily **HORMOGASTRINAE** Michaelsen, 1900.

Tubercula pubertatis (*xxvii*) *xix–xxiii* (*xxix*); spermathecal pores paired or multiple, 9/10/11/12/13/14/(15); 3 oesophageal gizzards.
2 genera containing 3 species.

Distribution. Sicily, Italy, Sardinia, Corsica, southern France and Spain; one species (introduced?) Algeria and Tunisia.

Subfamily **VIGNYSINAE** Bouché, 1970.

Tubercula pubertatis *xxi–xxiv*; spermathecal pores paired, 9/10/11; 2 oesophageal gizzards, anterior half of *vi* and by 6/7.

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*The similarities between *Ailoscolex* Bouché, 1969 and *Komarekiona* Gates, 1974 have not been recognized previously, possibly because of a printing error in Bouché's monograph (1972). In this work, the diagnosis of the family Ailoscolecidae included the statement "Glande de Morren présente" (p. 197), whereas in the account of the anatomy of *A. lacteospumosus* there is the conflicting statement "Glande de Morren absente" (p. 199). The absence of calciferous glands however, was previously established in the original descriptions of the family and species (Bouché, 1969 : 526, 529 & 530).

Single genus and species.

Distribution. Southern France (hinterland of Montpelier)

Family **LUMBRICIDAE** Rafinesque-Schmaltz, 1815

Earthworms: body mainly cylindrical sometimes with the posterior region depressed or infrequently body quadrangular, octagonal or trapezoidal in cross section; dorsal pores usually present, exceptionally (Diporodrilinae) replaced by paired, intersegmental, dorsolateral coelomic pores; clitellum usually saddle-shaped occupying 4–32 segments between *xvii* and *lii,* tubercula pubertatis present, band-like or papillose; male pores paired *xv,* rarely *xiii* or *xiv,* preclitellar; spermathecal pores paired in 2–8 furrows between 5/6 to 19/20 located anywhere between setal line *a* and near the mid-dorsal line (commonly 2 pairs present between setal lines *cd* in furrows 9/10/11); oesophageal gizzard absent; intestinal gizzard present in 1 or 2 segments in *xvii–xx,* preceded by a crop in a single segment in *xv–xvii*; calciferous glands intra-mural in some or all of (*ix*) *x–xv*; prostatic glands absent; spermathecae paired, adiverticulate, either interparietal or extending freely into the coelom; meganephridial.
Two subfamilies.

Distribution. Palaearctic region and eastern North America; some species introduced into other regions.

Subfamily **LUMBRICINAE** Rafinesque-Schmaltz, 1815.
Single dorsal pores present; intestinal gizzard confined to a single segment.
20 or more genera of disputed validities containing some 300 species.

Distribution. Palaearctic region (poorly represented in Asia) and a few species in areas of North America to the east of the Midwest lands once submerged beneath Cretaceous seas; about 10 mainly edaphophagous species inhabiting temporary burrows, introduced into other regions of the world.

Subfamily **DIPORODRILINAE** Bouché, 1970.
Single dorsal pores absent, replaced by paired, intersegmental coelomic pores; intestinal gizzard occupying two segments.
Single genus with 2 species.

Distribution. Corsica.

Family **LUTODRILIDAE** McMahan, 1976.

Earthworms of river-side or river muds: body quadrangular; dorsal pores absent; clitellum annular, occupying 35–51 segments (*xx*) *xxv–lxi* (*lxxi*), tubercula pubertatis paired, extending throughout most of the clitellar region, aliform; male pores paired *xxxii,* intraclitellar; female pores paired *xxiv*; spermathecal pores multiple 15/16–25/26; oesophageal gizzard absent; intestinal dilation present *xxi–xxiv*; calciferous glands absent; testes 10 pairs, *xii–xxi*; prostatic glands absent; ovaries paired in *xxiii*; spermathecae adiverticulate, multiple, interparietal; meganephridial.
Single genus and species

Distribution. Southeastern United States (southeastern Louisiana between the Mississippi and Pearl rivers).

Superfamily **BIWADRILOIDEA**

Freshwater worms: lateral line present between the dorsal and ventral setal couples; ovaries small, lobate (conical in young individuals), oocytes shed (?) individually, not forming

strings; calciferous glands absent; supra-oesophageal vessel present; subneural vessel absent; hearts lateral.
Single family.

Distribution. Japan.

Family **BIWADRILIDAE** Jamieson, 1971*a*

Freshwater worms: body cylindrical (swollen laterally in the region of the male pores); dorsal pores absent; clitellum annular, extensive (*xiv*) *xv–xxxi* (*xxxiv*), tubercula pubertatis absent, paired quadrangular porophores carry the male pores on *xiii*; spermathecal pores absent (conical to thecal-shaped spermatophores usually present in pairs near the male pores particularly on the dorsal and dorso-lateral body walls); gizzards absent; prostatic glands lobular *xiii*, in addition paired cylindrical setal glands discharge by the genital setae ventrally to the prostatic ducts; spermathecae absent; meganephridial.
Single genus and species.

Distribution. Japan in streams, rice paddies and lakes (Lake Biwa, 60 m).

Superfamily **GLOSSOSCOLECOIDEA**

Earthworms some freshwater exceptionally littoral: lateral line absent; ovaries large, elongately band or ribbon-shaped, tending to become lobate with several digitiform processes, oocytes not forming egg-strings; calciferous glands, when present, extra-mural; supra-oesophageal vessel usually present; subneural vessel, when present, free of the nerve cord, adherent to the parietes; some hearts latero-oesophageal.
Four families.

Distribution. America, Africa and Madagascar, southern India and southeastern Asia to western Indo-Australasian archipelago.

Family **KYNOTIDAE** Jamieson, 1971*a*

Earthworms: body cylindrical; dorsal pores absent; clitellum annular or saddle-shaped *xviii–xxxxvii*, tubercula pubertatis absent; male pores paired *xvi*, rarely *xv*, within copulatory pouches which when everted form clasper-like 'appendages', preclitellar; spermathecal pores inconspicuous, multiple 13/14/15/16; oesophageal gizzard *v*; intestinal gizzard(s) absent; calciferous glands absent; supra-oesophageal vessel present; tubular prostate-like setal glands associated with the copulatory pouches; spermathecae adiverticulate, multiple; meganephridial.
Single genus containing 12 or so species.

Distribution. Madagascar (primary forest).

Family **MICROCHAETIDAE** Michaelsen, 1900.

Earthworms: body cylindrical; dorsal pores absent; clitellum saddle-shaped extending 20 or so segments *ix–xxxiv*, tubercula pubertatis present, ridge-like or papillose; male pores paired behind *xvi*; intraclitellar; spermathecal pores sometimes absent otherwise inconspicuous, usually multiple, occasionally paired, in some or all 10/11–15/16; oesophageal gizzard *vii*; intestinal gizzard(s) absent; calciferous glands single pair near 9/10; subneural and supra-oesophageal vessels absent; prostatic glands absent, setal glands associated with the genital setae (copulatory sacs absent); spermathecae adiverticulate, sometimes serpentine; usually meganephridial with additional numerous coiled loops in the anterior segments which are often enteronephric, rarely (*Tritogenia*) 2 pairs of meronephridia in each segment.
Three genera containing 33 species.

Distribution. Republic of South Africa (primary grasslands).

Family **GLOSSOSCOLECIDAE** Michaelsen, 1900.

Earthworms exceptionally (*Pontoscolex*) on beaches perhaps littoral: body cylindrical; dorsal pores seldom present; four pairs of setae in each segment occasionally with the setal couples alternatively closely and widely paired in successive segments (e.g. *Pontoscolex*), rarely setae numerous (*Periscolex*); clitellum saddle-shaped occupying up to 12 segments beginning near *xiv,* tubercula pubertatis present; male pores inconspicuous sometimes within copulatory pouches, usually intraclitellar rarely post clitellar (*Opisthodrilus*), exceptionally 2 pairs (*Eudevoscolex*); spermathecal pores inconspicuous, usually paired, seldom multiple, mainly pretesticular occasionally including the testicular segments; oesophageal gizzard in *vi*; intestinal dilation in the region of *xvi*; calciferous glands extra-mural, 1–8 pairs between *vii–xiv*; supra-oesophageal vessel present; prostatic glands absent; spermathecae adiverticulate either interparietal or extending freely into the coelom; meganephridial.
About 25 genera containing nearly 200 species.

Distribution. Central America including many Caribbean islands and tropical South America (wide range of habitats, predominantly forest soils), *Pontoscolex* now circum-tropical on or near beaches.

Family **ALMIDAE** Duboscq, 1902.

Freshwater worms often in riverside muds: body quadrangular in cross-section, at least behind the clitellum, setal pairs commonly located near the angles; dorsal groove commonly present; dorsal pores absent; clitellum annular, variable length and location (*Callidrilus* 19–29 segments beginning in or behind *xii, Drilocrius* and *Glyphidrilocrius* 22–30 or so segments beginning near male pore *Glyphidrilus* 17–35 segments beginning in or near *xlii*; *Alma* 20–69 segments between *xxxv–ccvc*); tubercula pubertatis ridge-like (*Callidrilus*), aliform (*Glyphidrilus* and *Glyphidrilocrius*) or absent (*Alma* and *Drilocrius*); male pores inconspicuous, a single pair between *xv–xxx,* preclitellar or intraclitellar, sometimes near base of paired genital lobes (*Drilocrius*) or distally on paired ribbon-like claspers (*Alma*); spermathecal pores inconspicuous, multiple, intersegmental between *vii* to about *cc,* usually post-testicualr, especially numerous near setal lines; oesophageal 'gizzards' present as 1–3 dilations in *v–ix*; intestinal gizzards absent; calciferous glands absent; supra-oesophageal vessel present; 'prostatic-like' glands rarely present (*Callidrilus*); spermathecae adiverticulate partly or wholly interparietal; megnephridial.
Six genera (including *Areco* Righi, Ayres & Bittencourt, 1978) containing nearly 40 species.

Distribution. Tropical America, Africa, peninsular India, Burma, Malaysia and Indonesia eastwards to Sulawesi (aquatic or riverside muds).

Superfamily **MEGASCOLECOIDEA**

Earthworms, some associated with freshwater or exceptionally littoral: lateral line absent; ovaries large, fan to rosette-shaped with the oocytes forming several egg strings; calciferous glands extramural; supra-oesophageal vessel often present; subneural vessel, when present, free of the nerve cord and attached to the parietes. Some hearts latero-oesophageal.
Five families.

Distribution. Southern hemisphere (not Antarctica) and tropics also middle and western North America, eastern U.S.S.R., Japan, Korea and southern China; a few species of most families introduced into other regions.

Family **OCNERODRILIDAE** Beddard, 1891.

Earthworms often associated with freshwater: body cylindrical; dorsal pores seldom present; clitellum annular or saddle-shaped usually occupying up to 7 segments between *xii–xviii* exceptionally (*Nematogenia*) 13 segments in length extending backwards to *xxvi,* tubercula pubertatis absent but genital papillae and/or porophores common; male pores paired *xvii* or *xviii,* rarely *xix* or *xx,* intraclitellar or commonly by the posterior margin of the clitellum; prostatic pores 1–3 pairs between *xvi–xxi*; spermathecal pores pretesticular; 1 or 2 oesophageal gizzards; intestinal gizzards absent; calciferous glands *ix* and *x* (Ocnerodrilinae); supra-oesophageal vessel present; prostatic glands tubular with central canal, 1–3 pairs; spermathecae seldom diverticulate; meganephridial.
Two subfamilies.

DISTRIBUTION. Most of tropical America, both tropical and southern Africa, some Indian Ocean Islands, southern India and nearby areas; a few species introduced elsewhere, mainly tropical areas.

Subfamily **OCNERODRILINAE** Beddard, 1891.

Extra-mural calciferous glands present.
Twenty genera.

DISTRIBUTION. Western North America from the Tropic of Cancer southwards through Central America and some Caribbean islands into South America to near the Tropic of Capricorn, throughout Africa from the Nile Valley and south of the Sahara into Madagascar and the Seychelles.

Subfamily **MALABARIINAE** Gates, 1966.

Calciferous glands absent.
Three genera.

DISTRIBUTION. Peninsular India some species spreading into the Himalayan foothills and Burma.

Family **MEGASCOLECIDAE** Rosa, 1891.

Earthworms: body cylindrical; dorsal pores present; setae commonly four pairs on each segment sometimes numerous; clitellum annular or saddle-shaped usually occupying up to 7 segments between *xii–xviii,* tubercula pubertatis absent but genital marking and/or porophores common; male pores paired commonly on *xviii* (*xvii Nelloscolex* and *Tonoscolex,* rarely *xix* or *xx* in a few *Pheretima* s.l. spp.) immediately postclitellar; prostatic pores rare, usually prostatic ducts discharge through male pores, when present located on the same segment as the male pores (*Plutellus*) or more posteriorly (*Nelloscolex* and *Tonoscolex*); spermathecal pores paired or multiple, pretesticular; usually 1–3 oesophageal gizzards; intestinal gizzards rare (*Pleinogaster*), intestinal caeca sometimes present; calciferous glands often present; supra-oesophageal vessel(s) present; prostatic glands racemose in structure of mesoblastic origin without central duct, paired commonly in *xviii*; spermathecae usually diverticulate, paired or numerous; meganephridial or meronephridial.
About 25 genera containing over 1000 species.

DISTRIBUTION. Eastern U.S.S.R., Japan, Korea, southern China to Australasia; some species (especially of the genus *Amynthas*) introduced into other regions.

Family **ACANTHODRILIDAE** Claus, 1880.

Earthworms seldom freshwater, exceptionally on beaches or littoral: body cylindrical; dorsal

pores present; setae commonly 4 pairs on each segment, seldom 5 or 6 pairs, exceptionally numerous; clitellum annular or saddle-shaped frequently occupying up to 6 or 7 segments between *xii–xviii,* tubercula pubertatis absent but genital markings and/or porophores common; male pores usually paired on *xviii* with paired prostatic pores on both *xvii* and *xix,* or, paired on *xvii* or *xix* with a single pair of prostatic pores on the same segment, prostatic pores rarely more posteriorly, male pores mainly by the posterior margin of the clitellum or intraclitellar; usually 1–3 oesophageal gizzards occasionally rudimentary or absent; intestinal gizzards absent; calciferous glands common; supra-oesophageal vessel often present; prostatic glands tubular in structure of ectodermal origin with central canal, 1 or 2 pairs in *xvii* and/or *xix*; spermathecae usually diverticulate; meganephridial.
Over 20 genera.

Distribution. Americas, tropical and southern Africa,? southeastern Asia, Australasia, islands of the Southern Ocean.

Family **OCTOCHAETIDAE** Michaelsen, 1900.

Earthworms: body cylindrical; dorsal pores usually present; setae 4 pairs on each segment; clitellum annular or saddle-shaped frequently occupying 6–7 segments between *xii–xviii* seldom more extensive, exceptionally (*Agastrodrilus*) occupying about 30 segments; tubercula pubertatis absent but genital papillae and/or porophores common; male pores usually paired on *xviii* with paired prostatic pores on both *xvii* and *xix,* or, paired on *xvii, xviii* or *xix* with a single pair of prostatic pores on the same segment or confluent, exceptionally (*Hoplochaetella*) 2 pairs of male pores each associated with the prostatic pores on *xvii* and *xix,* or, 9 pairs (*Agastrodrilus*), male pores mainly situated by the posterior margin of the clitellum or intraclitellar; spermathecal pores pretesticular; usually 1–3 oesophageal gizzards sometimes rudimentary or absent; intestinal gizzards absent, intestinal caeca rare (*Millsonia*); calciferous glands common; supra-oesophageal vessel common; prostatic glands tubular in structure of ectodermal origin with central canal, paired in both *xvii* and *xix* or a single pair in *xvii, xviii* or *xix*; meronephridial.
Nearly 30 genera.

Distribution. Temperate species: Australasia. Tropical species: tropical America and Africa, peninsular India and into Burma; *Dichogaster* spp. introduced into other regions.

Family **EUDRILIDAE** Claus, 1880.

Earthworms: body cylindrical; dorsal pores absent; setae 4 pairs on each segment, the dorsal pairs frequently closer together than the ventral pairs; clitellum annular or saddle-shaped, frequently occupying up to 6–7 segments between *xii–xviii,* tubercula pubertatis absent but genital papillae and/or porophores common; male pore(s) single or paired on *xvii* or in 17/18 confluent with the prostatic pore(s), located principally by the posterior margin of the clitellum; 'spermathecal' pore(s) single or paired rarely pretesticular, usually post-testicular and sometimes confluent with the female pores, exceptionally behind the male pore(s); 1 oesophageal gizzard commonly in *v,* rarely reduced or absent; intestinal gizzards rare (invariably present when oesophageal gizzard reduced or absent); intestinal caeca absent; calciferous glands present; supra-oesophageal vessel present; prostatic glands tubular, single pair, commonly elongately ovoid, modified as 'euprostates', sometimes long and slender; spermathecae either modified and associated with the ovaries or absent and replaced by a 'spermathecal' system derived from mesoblastic tissue, the 'spermathecal' system extends from the 'spermathecal' pore(s) to the ovarian segment where it is confluent with the oviducts, occasionally continuing more posteriorly as a blind coelomic sac; meganephridial.
Two subfamilies containing some 500 species.

Distribution. Tropical Africa south of the Sahara; a species of *Eudrilus* has been introduced into other regions.

Subfamily **PAREUDRILINAE** Beddard, 1894.
Calciferous glands unpaired suboesophageal sacs; testes free.
About 15 genera.

DISTRIBUTION. Tropical Africa, mostly in eastern areas.

Subfamily **EUDRILINAE** Claus, 1880.
Calciferous glands unpaired suboesophageal sacs in *ix–xi* or *xi–xii* and a single pair of lamellate glands in *xii* or *xiii*; each testis enclosed in a 'sperm reservoir' formed from the ental end of the associated vas deferens which is confluent with the seminal vesicle in the succeeding segment.
About 30 genera.

DISTRIBUTION. Tropical Africa, mostly in western areas.

Systematic discussion

Criodriloidea. The ovaries of the single(?) species forming this superfamily are not well described but they are known to be small while the oocytes are shed individually and do not form egg-strings. The same characters are shared with the Biwadriloidea with which there is a further resemblance in the presence of two cerebral ganglia situated anteriorly in segments *i* and *ii* but the latter condition is possibly only the retention of the primitive state. (There are additional similarities with the Glossoscolecoidea but they are mainly in negative characters.) Authors have commented on the similarities between the Criodrilidae and the Lumbricidae: thickening of the musculature at the anterior end of the intestine, copulatory sacs at the ends of the sperm ducts, male pores occurring on porophores on segment *xv*, presence of spermatophores (structures common in the megascolecoid genus *Polytreutus*, family Eudrilidae), absence of a supra-oesophageal blood vessel and the subneural blood vessel adhering to the ventral nerve cord (for a fuller account and discussion, *see* Jamieson, 1971*a*). (Additional morphological resemblances with other groups, e.g. quadrangular body section, are seemingly adaptations to an aquatic environment and have little place in this present discussion.) However, if phylogenetic importance is attached to the association of the subneural blood vessel with the ventral nerve cord and to the absence of a supra-oesophageal blood vessel, it may be concluded that the Criodriloidea and Lumbricoidea are derived from a common ancestor with the less highly organized Criodriloidea retaining several primitive characters.

Lumbricoidea. The characters of the ovary and formation of a single string of oocytes are the primary features distinguishing this superfamily from the closely allied Criodriloidea while for separation from the Glossoscolecoidea and Megascolecoidea can be added the association of the subneural blood vessel with the ventral nerve cord and the negative features, the absence of both a supra-oesophageal blood vessel and extra-mural calciferous glands. Among the Lumbricoidea, the monotypic Lutodrilidae is unique in possessing paired testes in numerous successive segments. This multiplicity of testes segments should not be regarded as a primitive condition retained from some archaic ancestor but more simply seen as an aberrant specialization (a view which is supported by the unusual location of the ovaries in segment *xxiii*, another aberrancy). Members of the family Sparganophilidae possess features consistent with an aquatic mode of life, the rudiments of a lateral line and the absence of gizzards and calciferous glands, yet the body has not acquired a quadrangular cross-section which it has in the aquatic *Lutodrilus* and *Eiseniella*. The constituent families are recognized mainly on a few common characters which are expressed in varying combinations, a situation frequently encountered among allied taxa. The inter-relationships of the members of the superfamily are obscure. Isolation during the Quaternary glacial epochs may have provided conditions favouring change but in view of the wide range of the

Lumbricidae, it seems more likely that the families emerged long before those events (*see below* Discussion). Presumably the small families are themselves relicts of larger, possibly more diverse, wider ranging groups.

Biwadriloidea. Gates (1976*a*) placed the family Biwadrilidae in the superfamily Lumbricoidea on the similarities between the morphology of the ovary of a figured young individual of *Biwadrilus bathybates* (Stephenson, 1917) and his own observations on the immature ovary in the lumbricoid *Lutodrilus multivesiculatus* McMahan, 1976 (family Lutodrilidae). He did so only tentatively because details of budding oocytes were not illustrated (Gates, *personal communication*). In view of our uncertain knowledge of the morphology of the adult ovary and the shedding of oocytes in *B. bathybates,* the family Biwadrilidae becomes a doubtful candidate for inclusion in the superfamily Lumbricoidea. In many respects it more closely resembles the Criodriloidea not only in the characters of the ovary and the presumed absence of egg-strings but also in the possibly retained primitive character of the anterior situation of the cerebral ganglia in both segments *i* and *ii* and the absence of calciferous glands (structures invariably lacking in aquatic worms). It is however readily distinguishable from both the Criodriloidea and Lumbricoidea by the presence of a supra-oesophageal blood vessel, prostatic glands and a paired lateral line, the latter specialization being indicative of adaptation to an aquatic mode of life. (The only other Oligochaeta known to possess the rudiments of a lateral line are members of the lumbricoid aquatic family Sparganophilidae which further resembles the Biwadrilidae in having the primitive(?) condition of two pairs of latero-parietal vessels and the negative characters of the absence of a sub-neural vessel and spermathecae, the last being of doubtful significance in higher taxonomy.)

It is more likely that the affinities of the Biwadrilidae are revealed by the occurrence of the supra-oesophageal blood vessel, a structure known otherwise only from the mainly southerly occurring Glossoscolecoidea and Megascolecoidea in which the vessel is commonly associated with the extra-mural calciferous glands of terrestrial species. (In *B. bathybates* the vessel, named 'supra-intestinal' by Nagase and Nomura (1937), was described as 'attached directly to the dorsal surface of the alimentary canal, and is distinct in the segements anterior to IX.') It is however, conjectural whether this 'supra-intestinal' vessel in *Biwadrilus* is homologous or even analogous to the supra-oesophageal vessel in the southern earthworms. If homology is accepted, the presence of this blood vessel may not only provide evidence of affinity but possibly that the early forms possessed extra-mural calciferous glands and could have been terrestrial before more recent ancestors became secondarily adapted to an aquatic mode of life. This latter hypothesis however should be viewed with caution for although the aquatic Almidae also lack calciferous glands they too possess a supra-oesophageal vessel. Among other Glossoscolecoidea, the Kynotidae share the same characters but these worms are terrestrial while the Microchaetidae possess calciferous glands yet have no supra-oesophageal vessel.

Any discussion of the origins and antiquity of the group is further compounded by its currently restricted range, Japan, but *see below* Distribution. Presumably the present day Japanese populations are likely to be relicts of a once more widespread group. If the presence of the supra-oesophageal blood vessel is given systematic weighting, the origins would lie in Gondwana where certain of the Glossoscolecoidea and Megascolecoidea also possess this vessel. Possibly the group is of even greater antiquity than either of these two superfamilies and the mosaic of characters could indicate emergence at a time pre-dating the division of Pangaea. In view of the uncertainties surounding the origins and affinities of the family Biwadrilidae, it is prudent to place the family in a separate, monotypic superfamily.

Glossoscolecoidea. The three terrestrial families in this group form a homogeneous assemblage of geographically isolated African and South American earthworms; they differ from the mud-dwelling aquatic Almidae of the tropics of both the New and Old World mainly in the latter's adaptation to an aquatic environment and possessing specializations such as the development of claspers and alae which can evolve only when the restrictions imposed by a soil environment are removed. In addition to the characters of the ovary and the liberation of the oocytes, all four component families possess either or both a supra-oesophageal blood vessel and/or extra-mural calciferous glands. These characters separate them from members of the Criodriloidea and the Lumbricoidea while the absence of prostatic glands with ducts discharging through the male pores or onto adjacent segments, provides a ready means of separating the Glossoscolecoidea except for the Kynotidae, from both the Biwadriloidea and the Megascolecoidea. The origins of this superfamily seemingly lie in the southern hemisphere where members of the Megascolecoidea are dominant. Several fundamental characters are shared with this superfamily: the frequent occurrence of a supra-oesophageal blood vessel and (when present) extra-mural calciferous glands also the subneural blood vessel being free of the nerve cord and adhering to the parietes. Until Gates (1976*a*) recognized the discreteness of the Lumbricoidea, the mutual affinities of the southern families now forming the Glossoscolecoidea were obscured; it is now evident that this superfamily is more closely allied to the Biwadriloidea and the Megascolecoidea than to any other extant groups of earthworms.

Megascolecoidea. In addition to the characters of the ovary and the oocytes forming several egg-strings, members of this superfamily can usually be readily recognized by the male pores occurring by the posterior border of the clitellum, infrequently *xvii,* 17/18 (Eudrilidae), usually *xviii* or rarely *xix* and the presence of prostatic ducts discharging through or nearby to the male pores or onto adjacent segments. The superfamily forms the largest, most diverse and widespread of all earthworm groups. Two families, Ocnerodrilidae and Eudrilidae, are now universally accepted as discrete taxonomic entities but there is disagreement about the diagnostic criteria to be employed to delineate the groups here recognized as the separate families Megascolecidae, Acanthodrilidae and Octochaetidae. (Doubts about ranking have further obscured the fundamental problems confronting taxonomists.) To a large extent these three families are units of convenience, certainly the Acanthodrilidae and the Octochaetidae contain heterogeneous assemblages of genera whose relative distributions reflect the uncertain validities of the families. These apparently anomalous distributions are illustrated by the restrictions of the ranges of genera of the Octochaetidae into two groups, a temperate Australasian component and a tropical assemblage (the latter being largely sympatric with the family Ocnerodrilidae). There have been several attempts at classifying these non-Eudrilid megascolecoids by Omodeo (1958), Lee (1959) and Gates (1959) but the results have not been entirely satisfying while more recent proposals by Jamieson (1971*b*) employ taxonomic criteria which apparently require further investigation (Easton, 1979 : 17). Meanwhile it seems best to retain the (pragmatic) solution contained in the classification proposed by Gates (Sims, 1966). Part of the difficulty in classifying the component genera may be attributed to too few structures being seriously appraised as potential taxonomic characters and, more important, little consideration has apparently been given to the possibility that more than three families may be represented among the currently included genera.

Distribution

Ball (1975) seized on the controversy deriving from rival explanations of Omodeo (1963) and Gates (1929*a* & *b,* 1966, 1967, 1970) concerning the distribution of terrestrial oligochaetes in the northern hemisphere, to illustrate examples of biogeographical hypotheses. In doing so he drew attention to the problems of determining distributions caused by the occurrence of allochthonous species and went on to doubt whether biogeographical studies were possible on earthworms. It is true that such species may cause difficulties to the biogeographer but their importance should not be over-rated (Gates, 1976*b*). Most species of earthworms are highly adapted to their environments and transfer to another habitat can be deleterious causing death, cessation of reproduction or reduction in breeding rates so that new populations fail to become established. However, there are a few species which have wide environmental or feeding tolerances and it these which survive transportation and become established elsewhere. In some instances breeding is favoured as parthenogenesis is more prevalent among allochthonous populations than among autochthonous populations of the same species (Gates, 1956). A few species are spread naturally, i.e. without the intervention of man. The now ubiquitous euryhaline species *Postoscolex corethrurus* (Glossoscolecidae) from northeastern South America is found on or near many tropical and subtropical beaches around the world together with species of *Pontodrilus,* especially *bermudensis,* (Acanthodrilidae) whose origins are unknown, both seemingly are rafted around the tropics. Schwert & Dance (1979) also provided evidence of earthworms being transported by rivers. It is sometimes suggested that cocoons could be carried on the feet of migratory birds but successful transportation by this means seems improbable since cocoons are highly susceptible to desiccation which undoubtedly would occur during extended periods of flight. It is man however, who appears to have been responsible for the transportation of most allochthonous species although the number of species involved represents only a small percentage. Out of a total of some five hundred valid species of perichaetine Megascolecidae, about 15 species are allochthonous while from nearly three hundred species of Lumbricidae only about 10 can also be regarded as allochthonous. Significantly, the most numerous allochthonous Lumbricidae are edaphophagous feeders inhabiting temporary burrows, that is, they are not specialized feeders and are able to withstand disturbance in the soil which they inhabit. These characteristics stand them in good stead and enable them to colonize exotic cultivated soils following the local extinctions of native earthworms (Sims, 1978). Their success comes from their ability to exploit disturbed soils abandoned by native species and not from competing with the latter in their natural (undisturbed) environment.

The terrestrial Oligochaeta are slow-moving animals and being predominantly intolerant of saline conditions, the majority are incapable of bridging marine barriers without the intervention of man which is usually adventitious. They could therefore be regarded as excellent subjects for biogeographical study were it not for the lack of a fossil record. Not only is information on morphology, diversity and frequency of occurrence of ancestral populations no longer available but without fossils, evidence of past distributions has been irretrievably lost too. Without the knowledge of previous ranges, contemporary distributions have a reduced biogeographical significance. The present day absence of a group of earthworms form any area could be due to local extinctions or to the fact that the area had never been populated by their ancestors. Conversely, the presence of a group is equally enigmatic, it could provide evidence of the provenance of origin or merely of a successful recent colonization.

Despite the restrictions preventing valid conclusions being drawn from present day earthworm distributions, for the most part it is still possible to go some way to infer regions of origin. The suborder Lumbricina contains five superfamilies which occur throughout the world except for Antarctica. It may be assumed therefore that ancestral members of the suborder Lumbricina were widespread in the single palaeocontinent of Pangaea which formed at the end of the Palaeozoic from more ancient land masses. It was presumably with the break up of Pangaea and the ensuing isolation which favoured speciation that led to the evolution of the five superfamilies now recognized (and possibly other groups which are now extinct).

Euramerica

The supercontinent of Pangaea began to rift apart in the Triassic with the western extension of the Tethys Sea (Dietz & Holden, 1970) to form the northern continent of Laurasia and the large southern land mass of Gondwana. Subsequent sea-level changes in the north during the Jurassic led to marine incursions which eventually resulted in the formation of two isolated land masses joining by northern land connections what is now eastern North America with Europe and what is now western North America with Asia. The two continents so formed were named Euramerica and Asiamerica respectively (Cox, 1974 : 75). By the late Cretaceous, Euramerica extended from the eastern limits of the Mid-Continental Seaway of

North America to the western shores of the Turgai Straits which separated present day Europe from Asia (Tedford, 1974). The significance of these seas in animal distributions was recognized by Cox (1974) in studies on dinosaurs, Rich (1975) on birds and Platnick (1976) on spiders.

The Lumbricoidea occurs throughout the present day regions which once formed Euramerica. The greatest number of taxa are found in southern Europe, an area which escaped the faunal extinctions which affected the more boreal regions during the Pleistocene glaciations. The family Lumbricidae is not only distributed throughout this vast area but in addition it has spread into China where it is represented by four indigenous species and into Japan where there is a single indigenous species. It seems likely that the five present day indigenous Asian species could be derived from ancestors which successfully colonized parts of the East after the Cainozic closure of the Turgai Straits. The aquatic Sparganophilidae although essentially an Euramerican family, has now been recorded from widely separated localities in the United States but the present day range may have been affected by the development of recent drainage systems. A further complication is that these worms may be spread by man in the roots of water plants as seems likely from the rare records of the family in Britain and France; possibly other New World records, for example from Mexico and Guatemala, may also be due to man's intervention.

The distribution of the family Ailoscolecidae in Euramerica illustrates the affect that plate movements have had on animal distributions. Two genera are known from geologically associated localities in southern Euramerica but subsequent rifting caused members of the family to become widely parted spatially. The genus *Ailoscolex* is now found only in southwestern France while the genus *Komarekiona* inhabits parts of the southeastern United States.

Two other families, Hormogastridae and Lutodrilidae, have ranges consistent with the distribution of the family. The Hormogastridae occurs in countries bordering the western Mediterranean while the Lutodrilidae has been recorded from river or riverside muds in the southeastern United States. In the case of the latter, its present day distributions may differ from its original range since being associated with rivers, individuals may have been carried downstream to colonize new areas as new drainage system developed.

The aquatic monotypic superfamily Criodriloidea is also confined to parts of southern Europe. It occurs therefore in a region where the greatest number of genera and species of its close ally, the Lumbricoidea, have been recorded.

Gondwana

The division of Pangaea in the Triassic not only resulted in the separation of Laurasia from Gondwana but by the close of the era, 180 m.y.a., the latter was split into West Gondwana comprising South America and Africa including Madagascar, the East Gondwana consisting of Antarctica, Australasia and, by then, a detached Peninsular India (Dietz & Holden, 1970). Additionally a single mid-Permian(?) land mass, Pacifica, originating to the east of Australia and Antarctica had split into three groups of fragments; the Kula fragments drifted northwards, the Farallon fragments northeastwards and the Phoenix fragments eastwards (Nur & Ben-Avraham, 1977). By the late Jurassic, 135 m.y.a., the South Atlantic Ocean had begun to open in West Gondwana, a process which continued through to the late Cretaceous, 65 m.y.a. by which time the land connections between western Africa and eastern South America had been severed. Contemporaneously(?) in East Gondwana, the fragments of Pacifica had by then travelled vast distances, the Kula fragments collided with Alaska and eastern Siberia, the Farallon fragments with western North America and the Phoenix fragments with western South America. Although New Zealand had become detached from western Antarctica by the late Cretaceous, the separation of Australia from Antarctica had only just started, a process which continued well into the Oligocene. During this era, peninsular India which had been slowly rifting northwards since the Triassic, was spanning the equator at the fringe of the southwestern limits of the Asian plate (Tedford, 1974); this trek continued until the Neogene when the Indian plate encountered and underthrust the southern margin of Asia, throwing up the Himalayan fold belt by the collision.

The superfamily Megascolecoidea occurs throughout the vast region derived from Gondwana, the family Acanthodrilidae is nowadays the most widely distributed of the group being absent only from tropical South America. The Acanthodrilidae is represented additionally in North America, by *Diplocardia* and *Argilophilus* (a close relative of the Australasian *Plutellus*) but this distribution may be due more to the Farallon fragments transporting ancestors from the southern palaeocontinent of Pacifica to the northeast than to colonization from South America. The possible importance of the transoceanic rifting of fragments of Pacifica to earthworm distributions is seen in the present range of the family Megascolecidae. Although essentially an Australasian group which has spread through the Indo-Australasian archipelago, this family provides the majority of earthworm species in the Kuriles, Japan, Korea and China. It seems more plausible that their ancestors arrived in these areas on the Kula fragments of Pacifica than by any other agency. (A hypothesis which assumes that the family was not once more widely ranging before widespread extinctions occurred.) The present distributions of the more enigmatic and probably artificial family Octochaetidae, may either reflect the spuriousness of recognizing the family taxonomically or merely illustrates the effect of extinctions, for nowadays it comprises temperate species inhabiting Australasia and tropical species occurring in America, Africa and Peninsular India into Burma. The family Ocnerodrilidae is essentially a family of the American and African tropics but interestingly the three genera which form the subfamily Malabarinae, represent the family in peninsular India. If extinctions have not obscured the situation, then presumably the differentiation of the subfamily followed the early rifting of peninsular India from the ancient southern supercontinent. The family Eudrilidae is confined to tropical Africa. Whether the family once had a wider range is problematic but the evidence of numerous genera in western Africa, mostly with limited ranges, leads to a conclusion that the family is currently undergoing a radiation and that it could be newly emergent in the area (*see below* Glossoscolecidae).

The other large superfamily of Gondwana, Glossoscolecoidea, contains four families of which three are soil-dwelling and are found in discrete geographical regions. The family Kynotidae in Madagascar, Microchaetidae in the somewhat arid savannah of southern Africa and the Glossoscolecidae in the forests and mountain grasslands of Central, tropical and subtropical South America. Again if the possibility of extinctions is ignored, then the emergence of these families presumably followed the separation of Madagascar from mainland Africa and the final severance of land links between Africa and South America. It is more probable however that extinctions have occurred. The Amazon basin, for example, provides a rich environment for the Glossoscolecidae yet there are no glossoscolecoid terrestrial worms in the previously adjacent Zaire basin. (Possibly the present radiation of the Eudrilidae in western Africa may be connected with the absence of the Glossoscolecidae or close allies. The Eudrilidae may be seen to be actively exploiting niches left vacant after the extinction of terrestrial glossocolecoids whose disappearance may well have been hastened or caused by this more successful family or by environmental factors, for example, the marine incursions in the area during the Cretaceous (Fig. 2).

A further example of the probability of extinctions having occurred to affect the present range of the superfamily is seen in the present relict distribution of the Microchaetidae within South Africa. The pampas at comparable latitudes in South America contains no glossoscolecoids yet the environment is not entirely dissimilar to the South African veld, a habitat which itself has become reduced within historical times (Sims, 1978 : 672). The fourth family comprising the Glossoscolecoidea is the predominantly aquatic Almidae which, unlike other members of this superfamily, is widely distributed. The Almidae occurs throughout the muds of rivers and lakes in the tropics of the Americas, Africa, peninsular India and parts of southeast Asia being mainly sympatric with the megascolecoid Ocnerodrilidae and tropical Octochaetidae. Presumably its emergence, like those of the two megascolecoid families, pre-dated the division of southern India from the Gondwana

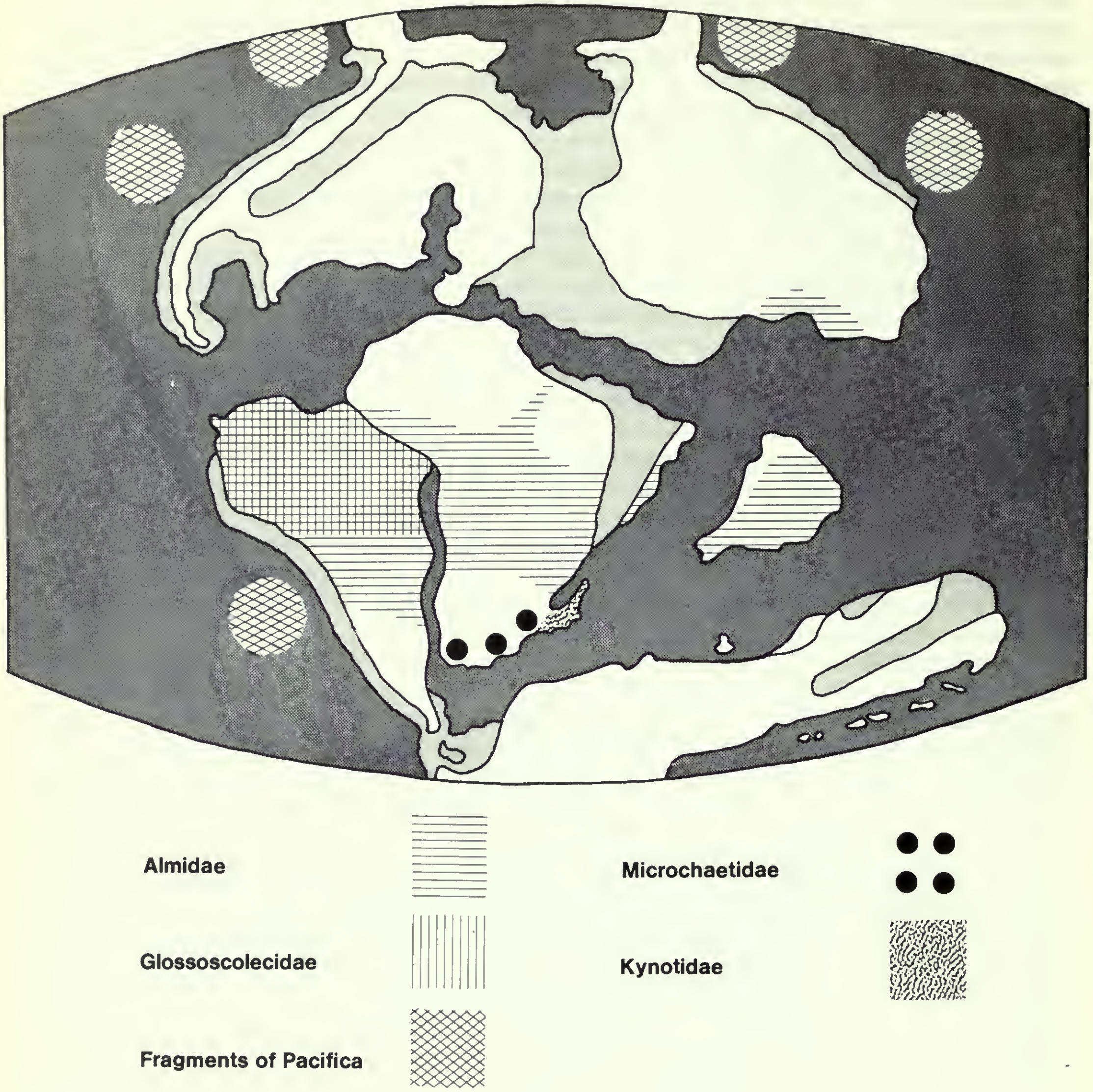
Almidae
Microchaetidae
Glossoscolecidae
Kynotidae
Fragments of Pacifica

Fig. 1 The distribution of land and sea at the end of the Jurassic 135 m.y.; a reconstruction of the continents with continental shelf and epicontinental seas after Tedford (1974); the locations of fragments of Pacifica superimposed according to Nur & Ben-Avraham (1977). The *present day* distributions of members of the superfamily Glossoscolecoidea are shown on the land areas.

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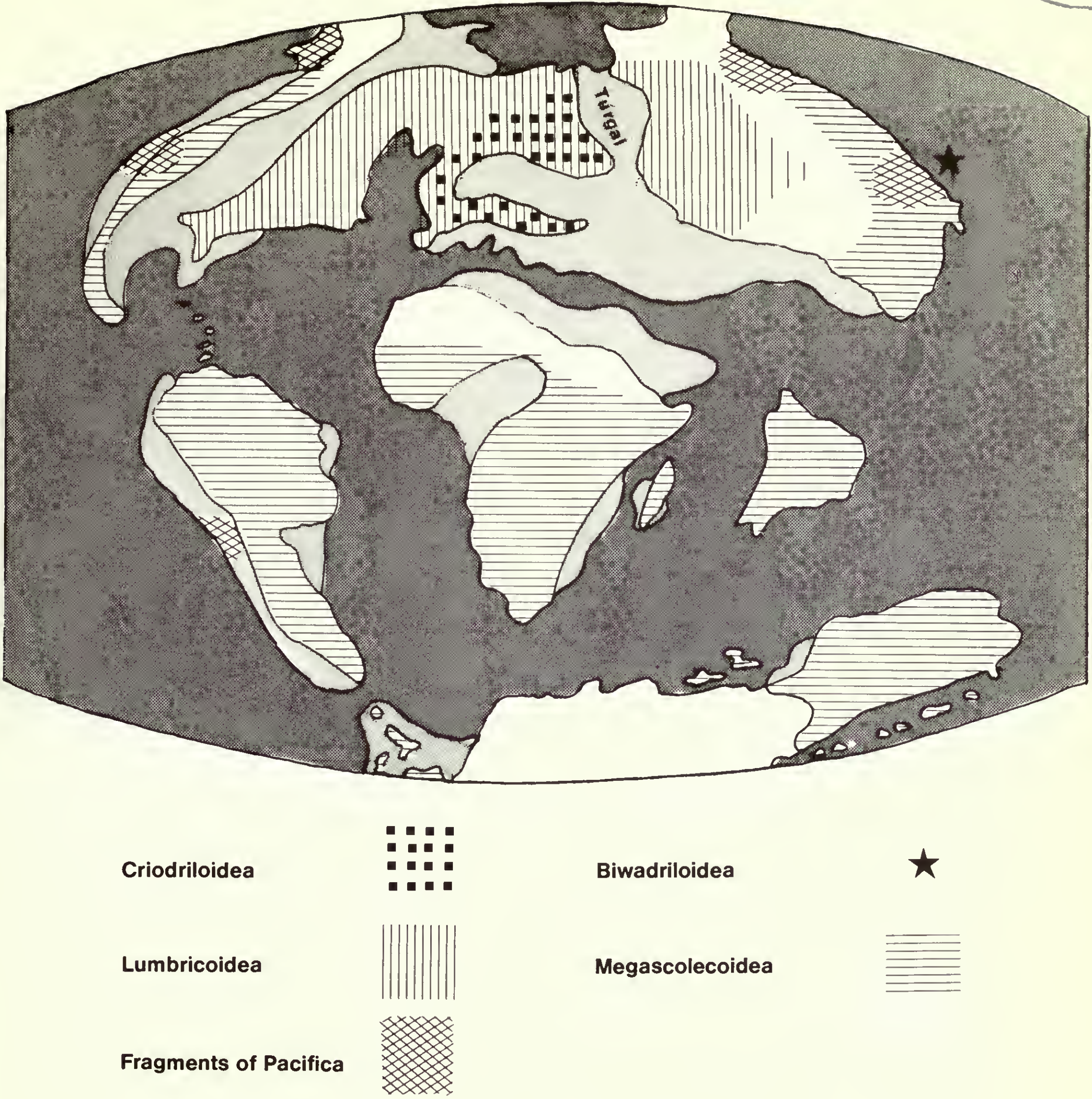
Túrgai
Criodriloidea ■
Lumbricoidea ▥
Fragments of Pacifica ▩
Biwadriloidea ★
Megascolecoidea ▤

Fig. 2 The distribution of land and sea at the end of the Cretaceous 65 m.y.: a reconstruction of the continents with a continental shelf and epicontinental seas after Tedford (1974); the locations of fragments of Pacifica superimposed according to Nur & Ben-Avraham (1977). The *present day* distributions of members of the suborder Lumbricina other than the subfamily Glossoscole-coidea, are shown on the land areas.

Erratum. This page replaces 121 in *Bull. Br. Mus. Nat. Hist.* (Zool.) **39**(2): 103–124.

mainland and the opening of the southern Atlantic Ocean. The family Almidae also extends from Asia along the Indo-Australasian archipelago as far as Sulawesi. This distribution may provide evidence that formerly the family and superfamily were widespread throughout the whole of Gondwana including Australasia but subsequently extinctions occurred in the east. Alternatively, the eastward extension of range from India could have been effected during the Oligocene when peninsular India passed close by southeast Asia during its stately progress northwards. After first invading the Asian plate, opportunity for further colonizations occurred during subsequent sea-level fluctuations, for example during the Miocene and early Pleistocene when at times the South China Sea was no more than a river valley (Fitch, 1954).

The smallest superfamily is the monotypic Biwadriloidea whose single species is now confined to rivers and lakes in Japan. On its morphology, this worm shows a close affinity with the austral Megascolecoidea and Glossoscolecoidea; it would seem therefore to be a relict of stock derived from Gondwana. If this conclusion is correct then it may be postulated that its ancestors populated the mid-Permian portion of Gondwana, Pacifica, which eventually split into several pieces. These worms, like some Megascolecoidea, were transported at least by the Kula fragments now located in eastern Siberia and Alaska. As mentioned above, the possibility that this group emerged before the late Palaeozoic break-up of Pangaea cannot be excluded.

Postscript and Acknowledgement

Studies on the classification of earthworms reported here originated partly from a long held personal dissatisfaction with Lumbricine systematics but more immediately to meet a publisher's requirement to provide a diagnosis for each category of the megadriles from subfamily upwards. The latter request was so reasonable that it was incumbent on me to accede but with the knowledge that a re-appraisal of the classification of the Lumbricina could not be delayed further. The most promising contribution on this topic had already been made by the doyen of oligochaetology, Dr G. E. Gates in his (1976*a*) paper on the Lumbricoidea, 'On earthworm ovaries and their importance in megadrile systematics. I'. Accordingly a preliminary survey was made of the Lumbricina centred on the group of characters which Gates had employed to define the Lumbricoidea. Then correspondence with Dr Gates elicited the information that because of ill-health and advancing years, Part II of his planned series of papers on the systematic importance of earthworm ovaries would never be published; however as our general conclusions were in agreement, he generously provided a digest of relevant observations and his opinions on megadrile classification for whatever use could be made of them. The present paper therefore owes much to the cooperation and goodwill of Dr Gates to whom I am deeply grateful for so willingly relaying his views to me. Nevertheless, as in any healthy, fruitful discussion we did not agree on all matters, so in several details I am claiming an author's prerogative and have expressed my own views; of these I absolve Dr Gates from responsibility should they be found wanting.

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Contents

	Page
Notes on some Difflugiidae (Rhizopodea: Protozoa) from Norfolk. By C. G. Ogden	125
The genus *Azygocypridina* Sylvester-Bradley (Crustacea: Ostracoda) with particular reference to *A. imperialis* (Stebbing, 1901). By J. Athersuch	139
Descriptions of two new and one poorly known species of the genus *Caligus* Müller 1785 (Copepoda: Siphonostomatoida). By G. A. Boxshall and A. R. Gurney	161
A revision of the spider genus *Onomastus* (Araneae: Salticidae). By F. R. Wanless	179
The genus *Atropacarus* Ewing (Acari: Cryptostigmata). By B. W. Kamill and A. S. Baker	189
The first record of a rare murine rodent *Diomys* and further records of three shrew species from Nepal. By J. M. Ingles, P. N. Newton, M. R. W. Rands and C. G. R. Bowden	205

Notes on some Difflugiidae from Norfolk (Rhizopodea, Protozoa)

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Introduction

The first British records of Rhizopoda and Heliozoa were contained in a privately-printed volume (Brightwell, 1848). The book comprised records and drawings of infusoria found by Brightwell in Norfolk, amongst which was the description of a species of *Difflugia*, tentatively identified as *D. globulosa* Dujardin. The only other records of *Difflugia* in the eastern counties of England are contained in Cash & Hopkinson (1909), otherwise the region has been neglected. The present paper is part of a series dealing with species belonging to the genus *Difflugia*, and is concerned with spherical or ovoid specimens which were isolated from a sample collected at Woodbastwick Fen, Norfolk. Three species of *Difflugia* were abundant in the sample, namely, *D. gramen* Penard, 1902; *D. lobostoma* Leidy, 1879 and *D. tuberculata* (Wallich, 1864) whilst two, *D. achlora* (Penard, 1902) and *D. wailsei* nom. nov. were represented by only a few specimens. The opportunity has also been taken to describe another member of the family Difflugiidae, that is *Cucurbitella mespiliformis* Penard, 1902, which was present in the same sample.

Materials and methods

A sample of algae and water plants was collected from a drainage dyke adjoining a reed marsh, at Woodbastwick Fen, Wroxham, Norfolk, in August, 1979. Specimens were extracted using a glass micropipette, washed in distilled water, and prepared for scanning electron microscopy using the techniques described by Ogden (1979*a*). Prepared stubs were examined on a Cambridge Steroscan S180 operating at 10kV and the results recorded on Ilford HP5 film.

Results

Difflugia gramen Penard, 1902

The shell is transparent, sometimes light brown in colour, spherical but tapering slightly near the aperture (Fig. 1). Although the general outline is usually constant, the texture of the shell varies between rough and smooth which may occasionally distort the outline. It is composed of a mixture of small to medium pieces of quartz, so arranged to make it intermediate in strength between fragile and robust. The particles are bound together by organic cement, small areas of which are frequently seen as part of the shell surface (Fig. 6). The surface of the cement is made of a network with a connecting membrane between the mesh (Fig. 4). The aperture is trilobed and bordered by an irregular raised ridge of small particles which are cemented together (Figs 2 & 3). A ring of small pores, about ten or more in number, surround the aperture slightly below the border of small particles (Figs 3 & 5). These pores are distinct openings in the organic matrix of the shell wall, but are sometimes covered by a thin smooth membrane.

Bull. Br. Mus. nat. Hist. (Zool.) **39**(3): 125–138

Issued 27 November 1980

The measurements for individual specimens are shown in Figure 7 and the range is given in Table 1. The measurement for the diameter of the aperture is taken as the internal distance between any two lobes, as indicated in Figure 2.

Although *D. gramen* has been the subject of two recent works (Stepánek & Jiri, 1958; Gauthier-Lièvre & Thomas, 1958) the difference between this species and three similar species, namely *D. limnetica* (Levander, 1900), *D. lobostoma* Leidy, 1879 and *D. achlora* (Penard, 1902), have not been adequately explained. Penard (1902) listed the differences between these four species and separated them mainly on size, colour and the presence or absence of an apertural collar. The specimens described here are in good agreement with the original description of *D. gramen*, but are somewhat longer than previously quoted measurements. For example, Penard (1902) and Gauthier-Lièvre & Thomas (1958) examined specimens ranging from 60–80 μm, whilst Stepánek & Jiri (1958) and Vucetich (1973) gave measurements between 71–92 μm. Variation of the shape of the apertural lobes appears to be common and several examples are illustrated by Stepánek & Jiri (1958).

Table 1 Range of measurements (in μm)

	Length (L)	Breadth (B)	Diameter of aperture (Da)	B/L	Da/L
D. achlora	49–54	43–46	16–17		
n=2	(52–69)	(41–53)	(14–25)		
D. gramen	89–117	70–112	23–39	0·96 ± 0·07	0·34 ± 0·04
n=35	(71–92)	(53–65)	(17–28)		
D. lobostoma	123–186	103–166	32–60	0·87 ± 0·06	0·29 ± 0·03
n=44					
D. tuberculata	102–152	88–141	29–44	0·89 ± 0·10	0·29 ± 0·04
n=27					
D. wailesi	96–112	79–90	29–34	0·80 ± 0·03	0·30 ± 0·01
n=6					

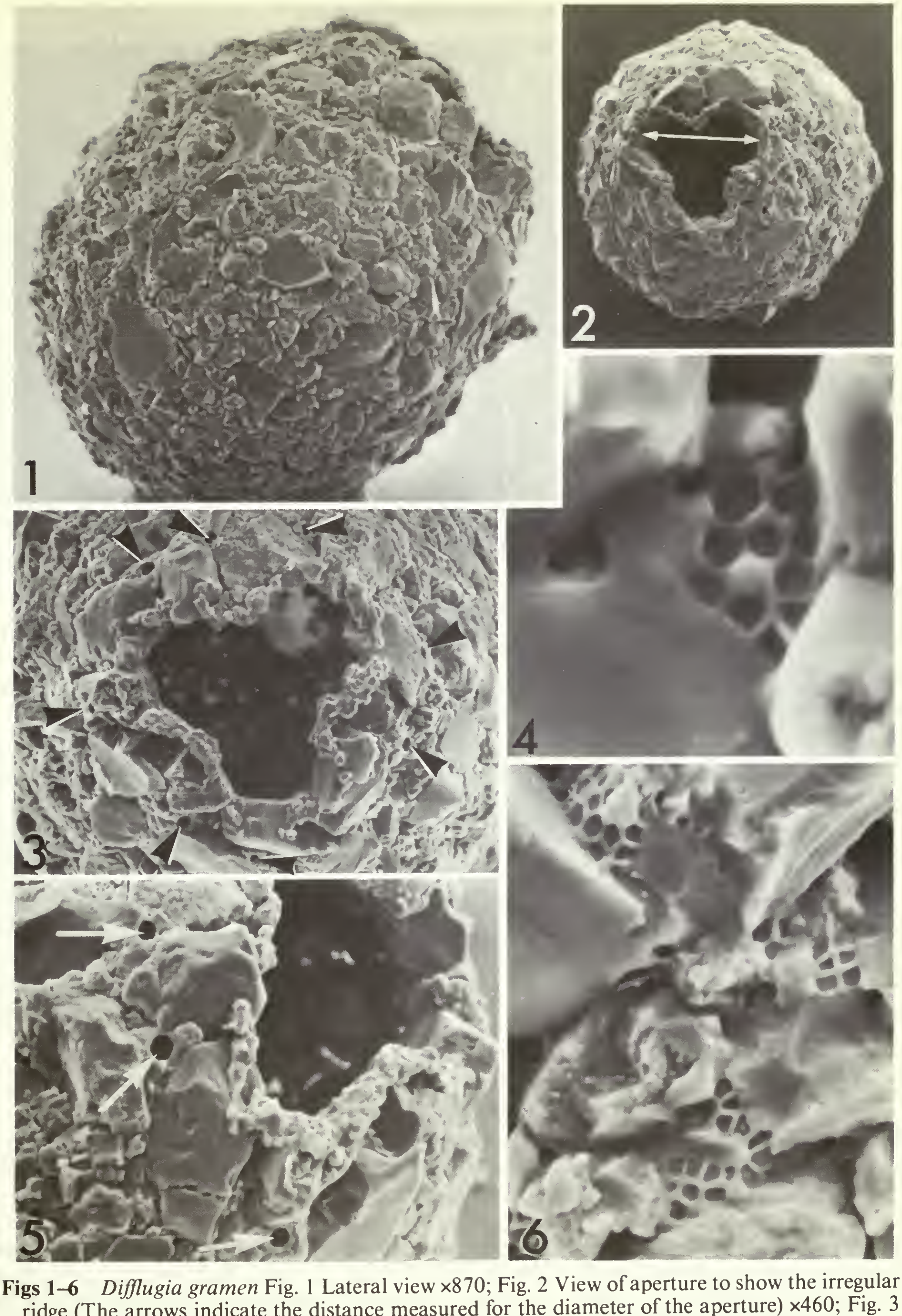
n= number of specimens measured
Bracketed measurements are taken from Stepánek & Jiri (1958).

Specimens of these species identified by Penard, in the Collections of the Department of Zoology, British Museum (Natural History), were examined for an apertural collar. It would appear that in lateral view specimens of *D. limentica* may have a small collar, whereas *D. gramen* and *D. lobostoma* have indications of some structure which could be considered to represent a collar. Unfortunately most of the specimens of these species are in lateral positions, as permanent preparations on slides, so that observations on the apertural opening are not possible.

Difflugia lobostoma Leidy, 1879

The shell is transparent, sometimes brownish in colour, ovoid or subspherical, and circular in cross section (Figs 8 & 9). It usually has a comparatively smooth outline, is robust and composed of a mixture of small to medium pieces of quartz. The quartz is bound together by organic cement which has the same structural network (Fig. 11) as that seen in *D. gramen* (Fig. 4). The aperture is usually trilobed and bordered by small particles (Fig. 10). Variation of the apertural opening ranges from squarish to curved lobes, the latter similar to those illustrated (Fig. 2) for *D. gramen*, and infrequently the aperture appears to be either four-lobed or as an irregular opening with indistinct lobes.

The measurements for individual specimens are shown in Figure 7 and summarized in Table 1.



Figs 1–6 *Difflugia gramen* Fig. 1 Lateral view ×870; Fig. 2 View of aperture to show the irregular ridge (The arrows indicate the distance measured for the diameter of the aperture) ×460; Fig. 3 Detail of aperture to indicate the ring of pores (arrowheads) × 1000; Fig. 4 Detail of organic cement network ×13000; Fig. 5 Side view of aperture to illustrate position of pores (white arrows) in relation to the apertural ridge ×1450; Fig. 6 Part of shell surface to show distribution of organic cement ×5300.

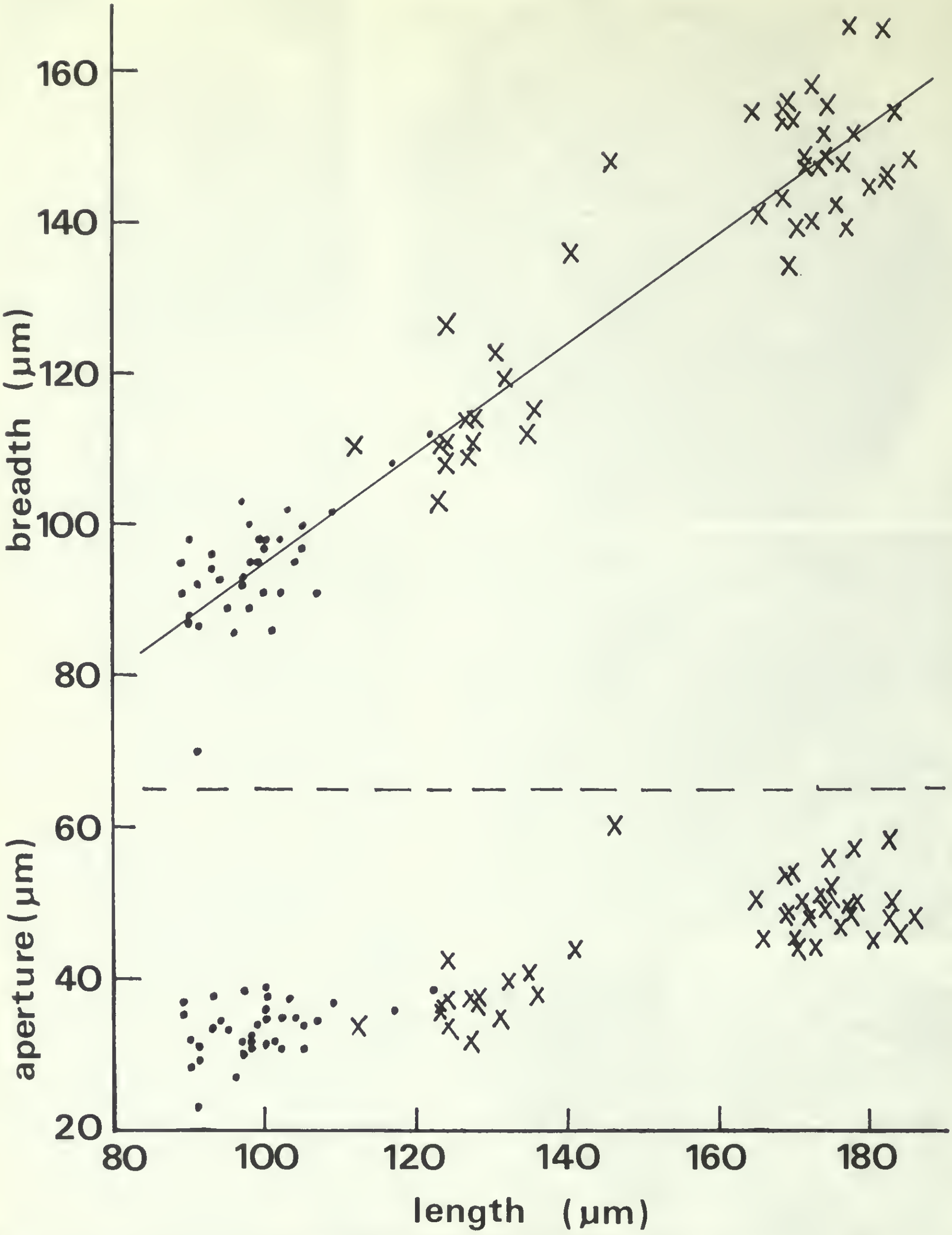
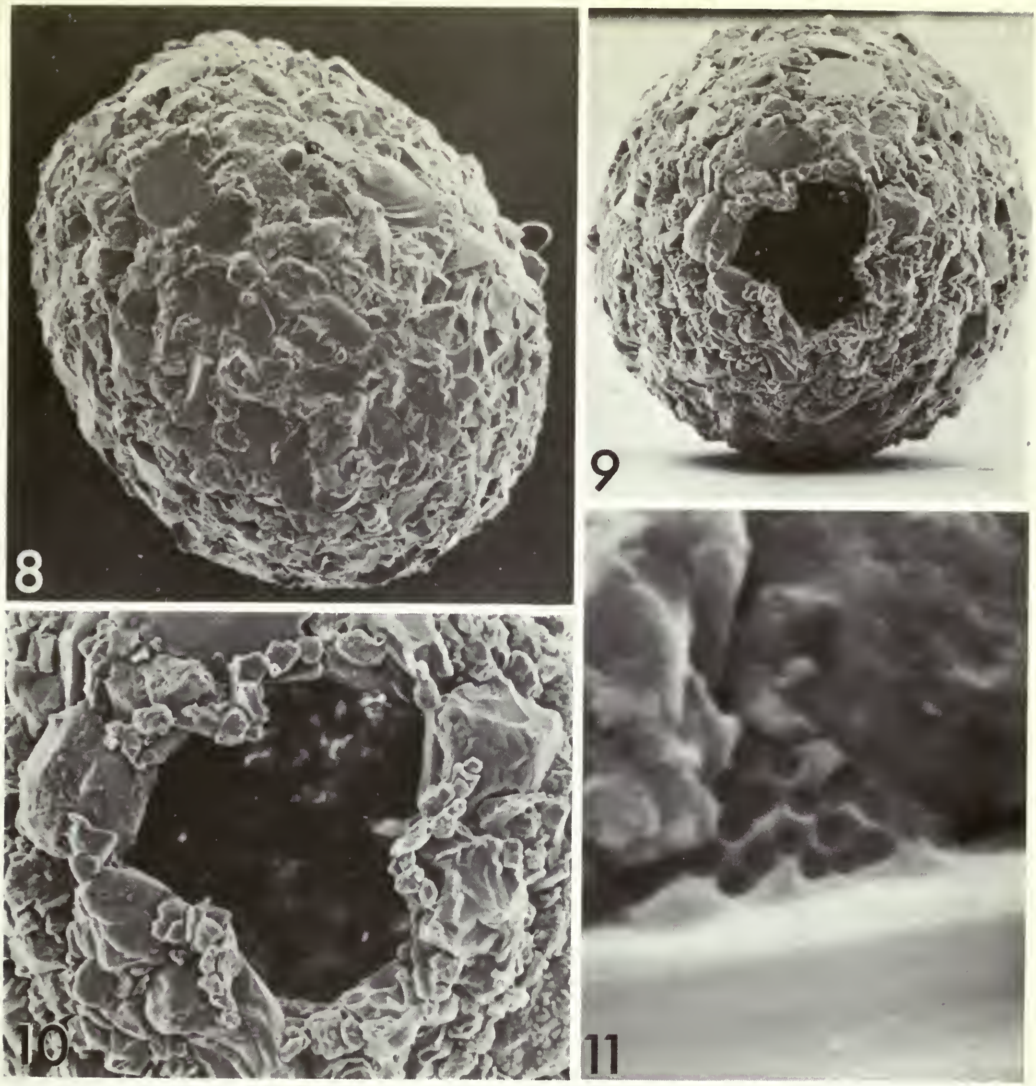


Fig. 7 Plot of individual measurements for specimens of *Difflugia gramen* (points) and *D. lobostoma* (crosses)—breadth (upper part) and diameter of aperture (lower part), vertical axis; total shell length, horizontal axis.

In the general description of *D. lobostoma*, Leidy (1879) described the shell as being usually composed of quartz-sand and rarely of diatoms or chitinoid material, whilst the aperture was usually from three- to six-lobed. His illustrations are so precise that we can identify at least five distinct species (*Difflugia achlora*, *D. gramen*, *D. tuberculata*, *Netzelia oviformis* (Cash, 1909) and *Cucurbitella mespiliformis*) amongst those that he attributed to represent *D. lobostoma*. Wailes (1912) identified some of the illustrations given by Leidy which at that time had been given specific names, but lists only *D. gramen* and *D.*



Figs 8–11 *Difflugia lobostoma* Fig. 8 Lateral view ×420; Fig. 9 Apertural view ×390; Fig. 10. Detail of aperture to show incomplete ridge of small particles ×900; Fig. 11 Portion of shell surface to show organic cement matrix ×10000.

tuberculata from the description of *D. lobostoma*. Unfortunately, the original description has not been amended to exclude those features that have since been considered to be the diagnostic characters of other named species, even though in his discussion Leidy (1879) indicated the most common features and measurements for *D. lobostoma*. The opportunity is taken here to redefine *D. lobostoma* from the original description (Leidy, 1879) and to designate the type figures: *D. lobostoma*—shell usually ovoid, composed of angular quartz-sand, with a trilobed aperture, fundus rounded, about 120–140 µm long and 100–128 µm broad, Figs 1-4, Pl. XV (Leidy, 1879).

Penard's (1902) description of *D. lobostoma* agrees well with the original differing slightly in size, 140–170µm, and in the shape of the aperture which was stated to be four-lobed in the form of a cross, although the cross frequently had an irregular outline. The descriptions given by Cash & Hopkinson (1909) and Vucetich (1973) are in general agreement with both Leidy and Penard, but their specimens range in size from 90–115 μm and 65–110 μm respectively. The first authors, further suggest that the sinuous nature of the three to six-lobed aperture could be useful in separating these ovoid forms. Gauthier-Lièvre & Thomas (1958) have used the shape of the aperture to describe new varietys and forms.

Difflugia achlora (Penard, 1902)

Although only two whole and one broken specimen of this fragile species were found, it was considered desirable to describe them because of their contrasting shell structures. Both of the complete specimens have an elongated ovoid shell and an irregular trilobed aperture. The first is composed of a mixture of small pieces of quartz (Figs 12 & 13) and the second of a mixture of small diatom frustules and fragments of these siliceous structures (Figs 14 & 15). The organic cement that binds the shell components together, in both cases, is in the form of a network (Figs 16 & 17). The diameter of the mesh is about 0·02 μm, which is about half the diameter of the mesh of both *D. gramen* and *D. lobostoma.* A few small particles are seen surrounding the apertural opening, and a few pores are present in the shell just posterior to the aperture. The measurements are given in Table 1.

The specimens described here are similar to those described by Penard (1902), except that neither of the present specimens have a collar, which was a diagnostic character of the original description. Penard described the casing as yellowish with brown veins dotted amongst the overlapping plates, these veins were later thought to be very small beads by Decloitre (1948), and it would appear that they were both probably commenting on the organic matrix of the shell.

Difflugia tuberculata (Wallich, 1864)

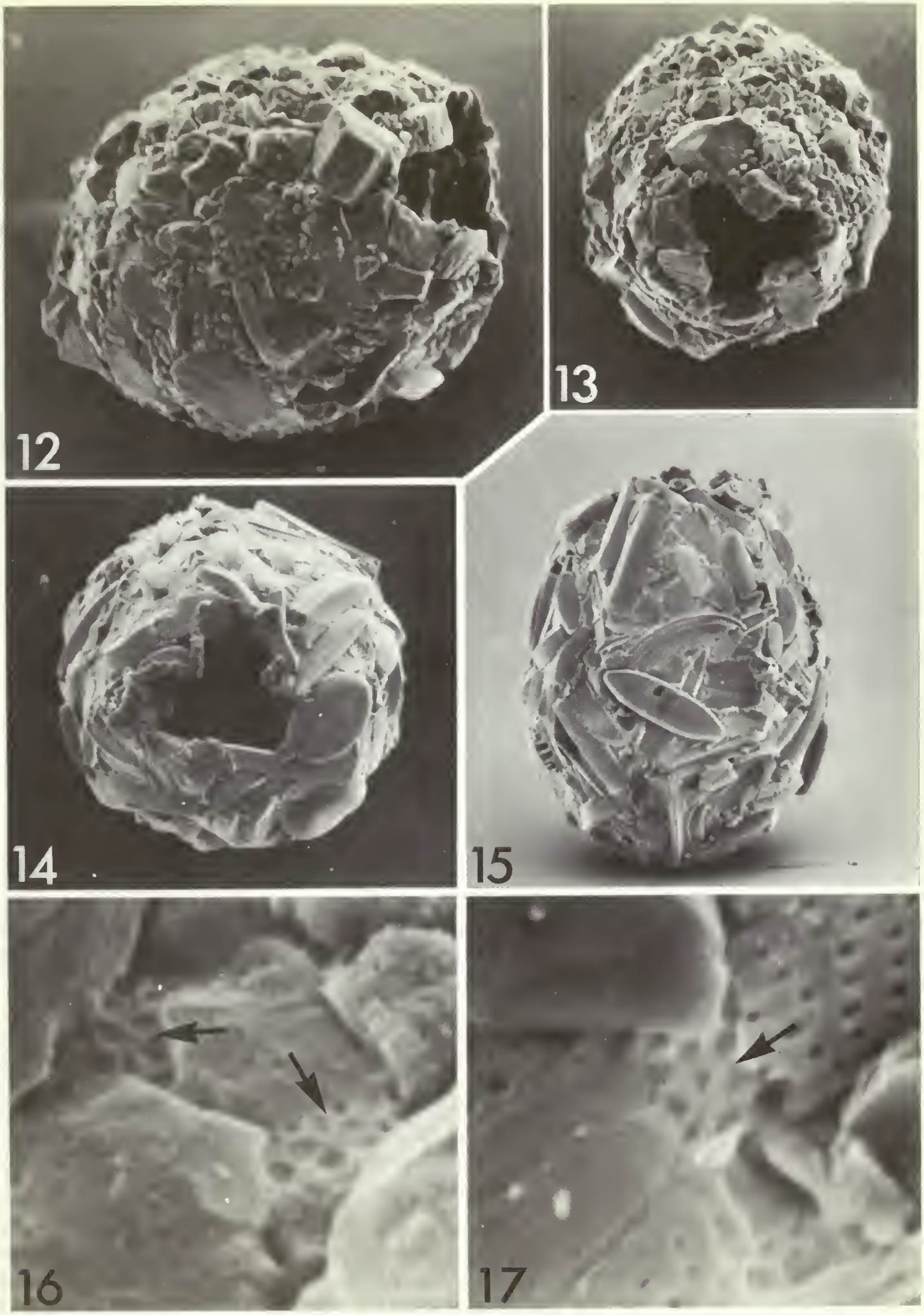
Our previous description (Ogden & Hedley, 1980) of this species was based on specimens whose shells were composed mainly of quartz particles. The present specimens have shells that are made mainly of diatom frustules, small siliceous elements and a few quartz particles. The outline is characterized by typical protuberances or bosses (Figs 18 & 19), whilst an abundance of organic cement in the form of a network, binds the shell particles together (Fig. 19). About ten small pores in the cement matrix, are arranged in a ring on the shoulder of the shell surrounding the aperture (Figs 21 & 22). A narrow projecting collar composed of small siliceous elements, surrounds the roughly circular aperture (Fig. 22). This collar is irregular and gives the apertural opening either an hexagonal or heptagonal appearance (Fig. 21), often these divisions are pointed or tooth-like (Fig. 20).

Penard (1902) noted specimens which he thought were polymorphic or transitional stages of *D. tuberculata*, and divided these into five groups on the basis of variation in the shape of the aperture and their different shell surfaces. Comments on variation of shell structure, from the present study, are included in the general discussion (see p. 135). Recently observations (Ogden, 1979*b*) on a few specimens from the Everglades, U.S.A., led me to suggest that the description of *D. tuberculata* might have to be amended to include specimens whose shells were composed mainly of diatom frustules. The present work has facilitated this emendment.

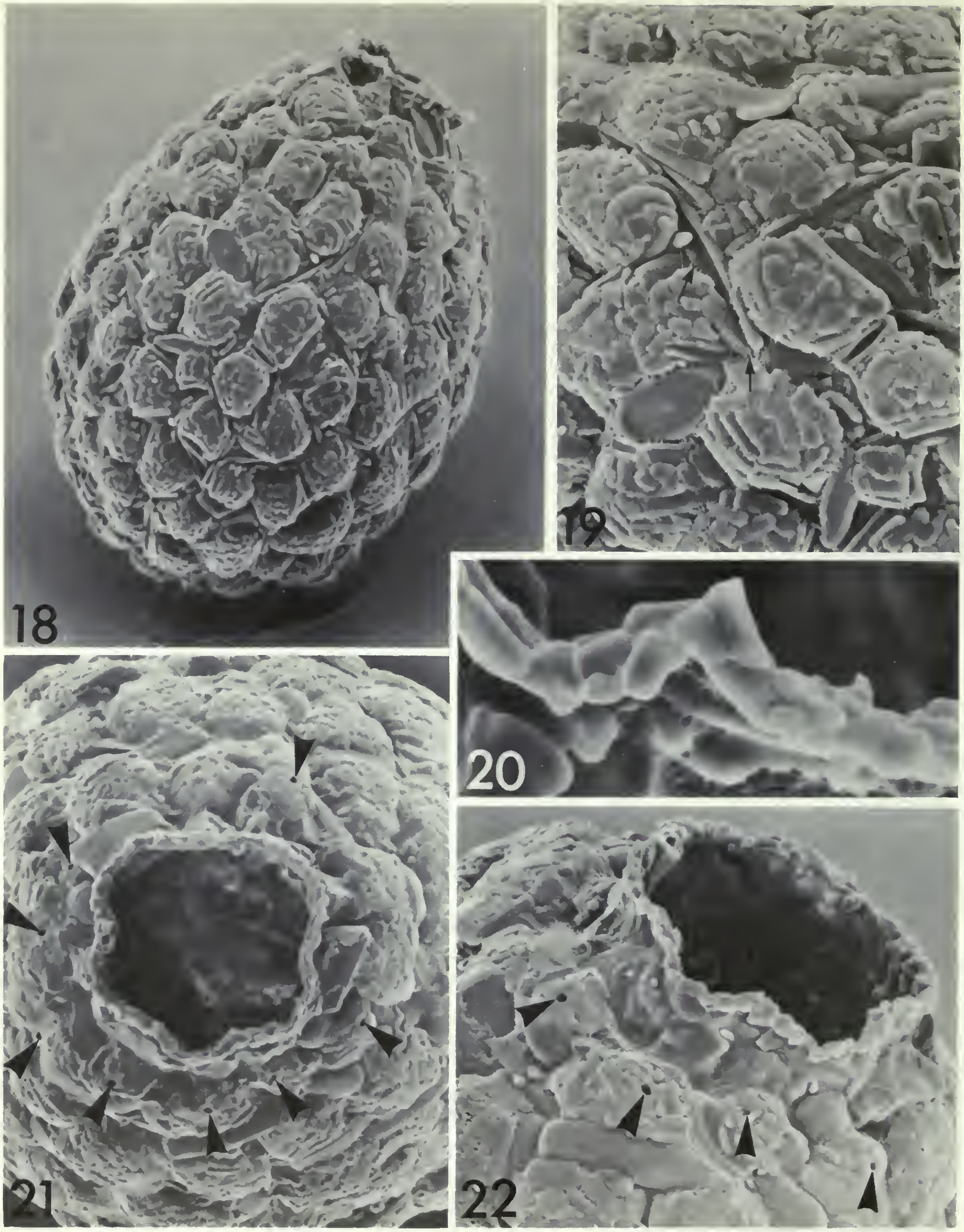
Difflugia wailesi nom. nov.

syn. *D. tuberculata* var. *minor* Wailes, 1919

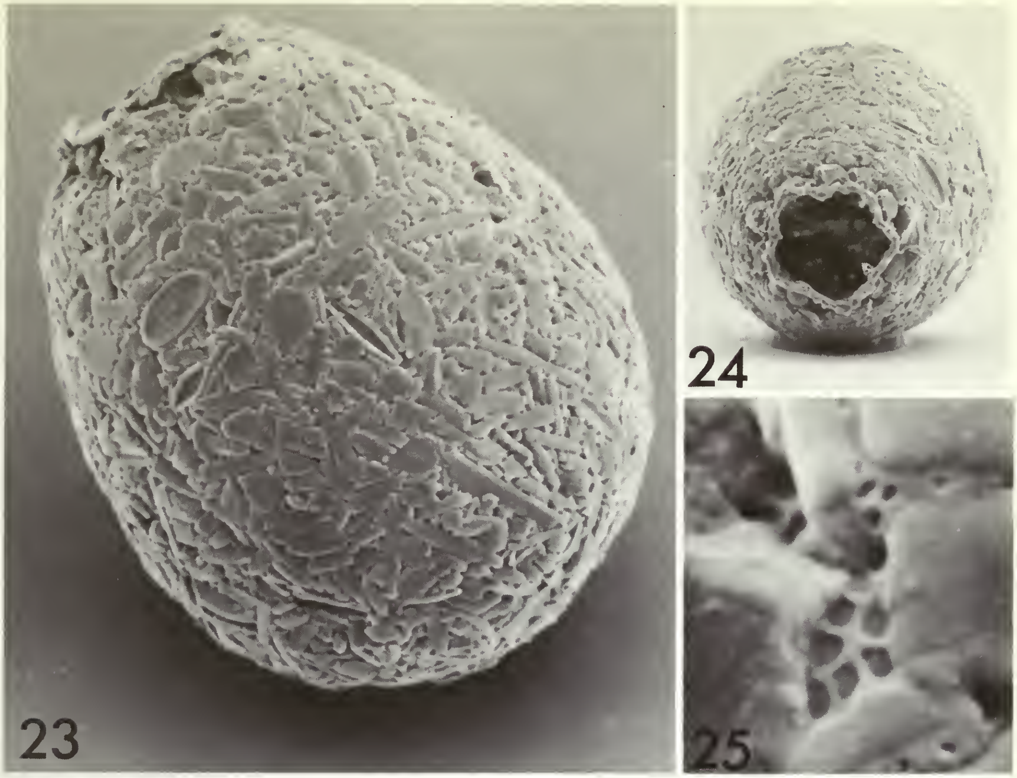
The shell is transparent, colourless, ovoid tapering towards the aperture (Fig. 23). It is fragile, has a smooth outline and is composed of a mixture of mainly diatom frustules and some flattened particles of quartz, bound together by a network of organic cement (Fig. 25). Just posterior to the aperture is a ring of small openings in the organic cement matrix, similar to those illustrated for *D. tuberculata* (see Fig. 21). The aperture is polygonal with either four or five indentations (Fig. 24) and is bordered by a slightly raised lip made of small particles cemented together.



Figs 12–17 *Difflugia achlora* Fig. 12 Lateral view of 'quartz' specimen ×1300; Fig. 13 Apertural view of 'quartz' specimen ×1100; Fig. 14 Apertural view of 'diatom' specimen ×1100; Fig. 15 Lateral view of 'diatom' specimen ×950; Fig. 16 Detail of organic cement ('quartz') ×12500; Fig. 17 Detail of organic cement ('diatom') ×14000.



Figs 18–22 *Difflugia tuberculata* Fig. 18 Lateral view to show typical protuberances ×580; Fig. 19 Detail of protuberances to indicate areas of organic cement (small arrows) ×1100; Fig. 20 Part of ridge that surrounds the aperture ×4100; Fig. 21 View of aperture to illustrate the ring of pores (arrowheads); Fig. 22 Side view of aperture to show position of pores (arrowheads) on shoulder of shell ×1200.

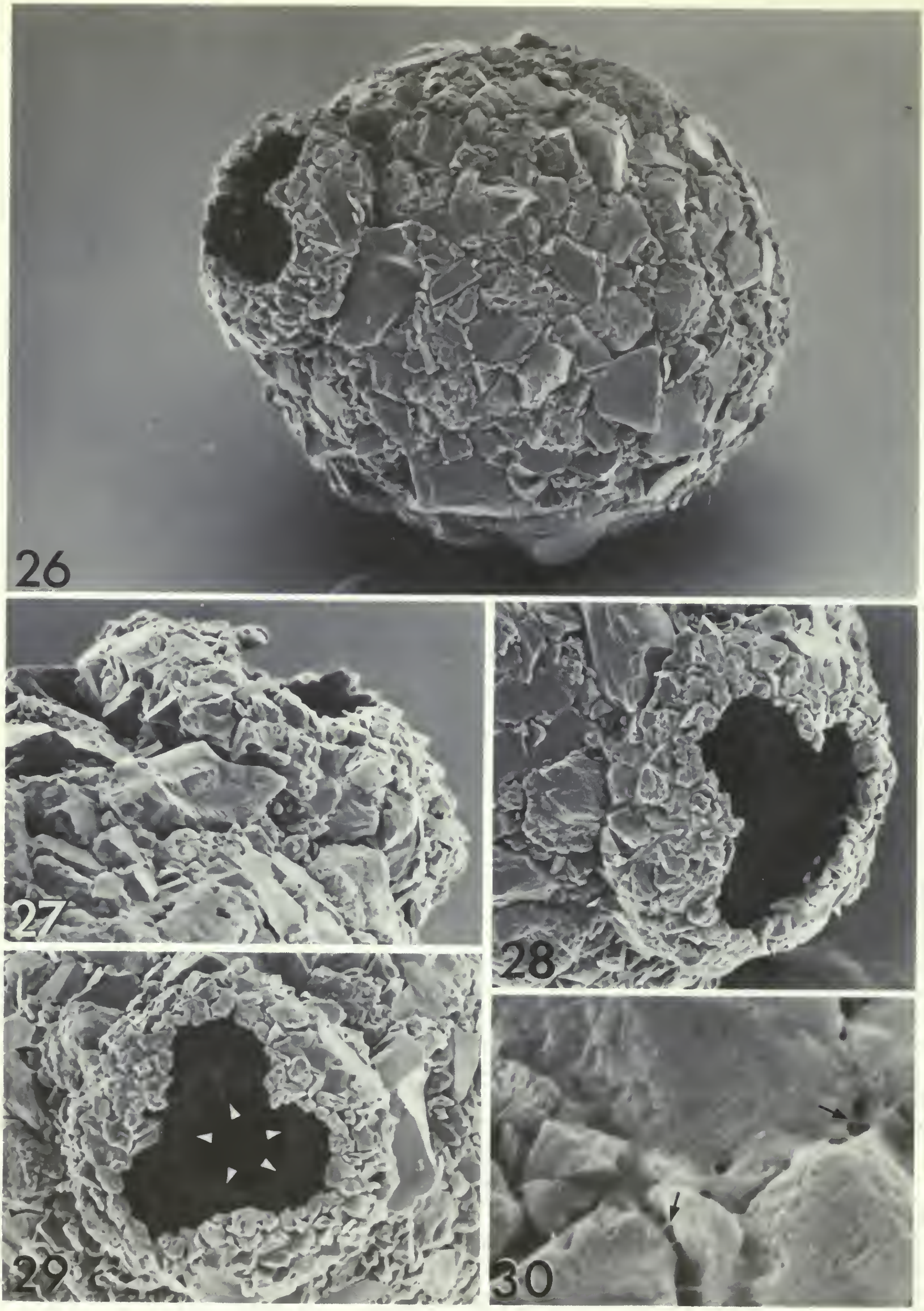


Figs 23–25 *Difflugia wailesi* Fig. 23 Lateral view to show smooth shell surface ×830; Fig. 24 Apertural view ×460 Fig. 25 Detail of organic cement network ×7700.

Penard (1902) described a small form of *D. tuberculata* which had a smooth shell. Specimens identical to these were listed as *D. tuberculata* var. *minor* by Wailes (1912), although the description of this variety appeared much later in Cash *et al.* (1919). In this latter work, Wailes refrained from describing these specimens as a distinct species because of Penard's (1902) earlier report regarding intermediate forms of *D. tuberculata*. More recently it was considered (Ogden, 1979*b*) that Penard's smooth specimens were possibly referable to the genus *Netzelia* Ogden, 1979. Confirmation of the correct generic status of this species must await evidence to show whether it can produce autogenous siliceous shell components, a prerequisite for the genus *Netzelia*, but this information can only be obtained from observations on this animal in culture. Until such information is available these smooth shelled specimens are here raised to species level in the genus *Difflugia*.

Cucurbitella mespiliformis Penard, 1902

The shell is dark grey or opaque, ovoid with a pronounced annular collar at the apertural extremity (Figs 26 & 27). It is composed of a mixture of small to medium pieces of quartz blended together to produce a strong shell with a relatively smooth outline. The organic cement that binds the particles is not very evident, but is occasionally seen at junctions (Fig. 30). The collar that surrounds the aperture usually has a regular three or four-lobed opening, but it may sometimes have a distorted outline, and is composed mainly of small pieces of quartz (Fig. 28). The divisions between the lobes may often appear as sharply pointed projections (Figs 28 & 29), due to the arrangement of small particles bordering the lobes. The aperture is a small roughly circular opening, on a level with the shoulders of the main shell



Figs 26–30 *Cucurbitella mespiliformis* Fig. 26 Lateral view to show apertural collar ×680; Fig. 27 Lateral view of apertural collar ×1200; Fig. 28 Latero-apertural view of apertural collar to illustrate the sharply defined projection dividing two lobes ×1100; Fig. 29 View of apertural collar to show the inner aperture opening (small arrowheads) ×1100; Fig. 30 Detail of shell surface, the small amounts of organic cement visible are arrowed ×7250.

walls, inside the annular collar (Fig. 29). The internal structure surrounding the aperture is composed of small pieces of quartz, hence the irregular opening. This inner apertural opening is covered by a smooth organic membrane in encysted specimens, but in some empty shells the recess of the collar is filled with small pieces of extraneous debris.

Range of measurements in μm (6 specimens examined): shell length 119–146, breadth 98–106, diameter of collar 33–49, length of collar 13–19, diameter of aperture 14–21.

In the original description (Penard, 1902) the collar was described as being four-lobed, and this was emended by Cash *et al.* (1919) to include both three and four-lobed specimens. In subsequent works (Gauthier-Lièvre & Thomas, 1960; Vucetich, 1973) the three-lobed specimens have been considered to represent a new variety and form, *C. mespiliformis* var, *africana* fma *triloba* Gauthier-Lièvre & Thomas, 1960. It is thought that this variation alone is insufficient to warrant specific identification and that these reports are best considered as *C. mespiliformis*.

The only previous British record of this species is from a pond at Husthwaite near York (Cash *et al.*, 1919), but it has been reported from Europe (Penard, 1902; Deflandre, 1927; Chardez, 1956; Thomas, 1954), America (Edmonson, 1912), South America (Vucetich, 1973; Boltovsky & Lena, 1974), and Africa (Decloitre, 1948; Gauthier-Lièvre & Thomas, 1960).

Discussion

In previous studies on pyriform specimens of *Difflugia* (Ogden, 1979*a*; 1980; Ogden & Fairman, 1979) it has been shown that size, shape and detailed shell structure can be used successfully to distinguish species. The application of these criteria as applied to five ovoid species are summarized below.

Whereas in the earlier work the shape and size of the aperture, was with few exceptions, a relatively uniform character, in ovoid forms this feature appears to be more variable. For example, although the aperture in specimens of *D. lobostoma* described here (p. 126) is generally trilobed with only a few specimens having ill-defined lobes, Penard's (1902) specimens were predominately four-lobed. It is possible that Penard's specimens represent a distinct species, but the aperture apart, his description is in good agreement with that for *D. lobostoma*.

The presence or absence of an apertural collar is another questionable diagnostic character. It is generally accepted that in most testate amoebae the aperture is formed initially during division to produce a daughter shell, and that the appearance of the remainder of the shell is accompanied by cytoplasmic movement between the parent and the newly-formed daughter. An effective junction between the two opposed apertures is therefore essential. As the apertural opening in both *D. gramen* and *D. lobostoma* is irregular, it is suggested that the small ridge of particles that borders the aperture is constructed in such a way so that it forms an effective seal between the parent and daughter shells during division in these animals. This would account for the uneven distribution of these particles around the apertural opening, and for the way in which they are often concentrated together to fill depressions or conversely to form projections. It follows that these ridges would not be identical, even between parent and daughter. In fact they vary considerably and their only real value as a diagnostic character is probably their presence or absence. This theory regarding the apertural ridges can only be tested by opposing the apertures of several parent and daughter shells, to establish whether or not such related couples match.

Although the ring of pores just posterior to the aperture in *D. gramen* is used here as a diagnostic character, being incomplete in *D. achlora* and absent in *D. lobostoma*, the function of this feature is unknown and must be used with some reservation. Its appearance in the same position in both *D. tuberculata* and *D. wailesi* certainly rules out any suggestion that it is an artifact.

The measurements given for individual specimens of *D. gramen* and *D. lobostoma* from Norfolk, would suggest that they can be separated using these parameters (see Table 1). If these measurements are presented in graphical form however, it would appear that in length and breadth, at least, there is a similarity between the two species that suggests a correlation. The slope of a line fitted by eye to all the data, would also seem to fit the data if it was treated as two separate parts. This similarity is also shown in Table 1 by comparing the ratio B/L (breadth ÷ length). The diameter of the aperture is included in the graph and as a ratio (see Table 1), but these results do not appear to be significantly different.

Stepánek & Jiri (1958) measured a hundred specimens of both *D. achlora* and *D. gramen*, and suggested that the shells of these two species appeared to be significantly different in length and breadth (see Tables 1 & 2). If the individual measurements are plotted (Fig. 31), a similar correlation between length and breadth can be shown between these two species to that illustrated for *D. gramen* and *D. lobostoma* (Fig. 7).

Table 2 Mean values (in µm)

	Length	Breadth	Diameter of aperture
D. achlora	(60·8)	(47·2)	(21·4)
D. gramen	98·8	94·3	33·6
	(81·6)	(60·4)	(25·4)
D. lobostoma	158·1	137·3	45·7

Bracketed measurements are taken from Stepánek & Jiri (1958).

By plotting the data for breadth and length in this way, it could be inferred that specimens of *D. achlora*, *D. gramen* and *D. lobostoma* exhibit progressive steps in size that possibly represent one species. Variability in the recorded measurements of *D. gramen* and *D. lobostoma* have already been mentioned (p. 126). Such differences illustrate how difficult it is to separate three similar species on size alone, and suggests that the incorrect specific designation has probably been given on several occasions. Furthermore, the suggestion that *D. achlora* and *D. gramen* could be distinguished by morphometric and statistical methods (Stepánek & Jiri, 1958), could also be interpreted as a way of differentiating between two populations of the same species, especially as the specimens of each species came from two different sources.

The present work does not help to resolve this problem, and measurements are used here to distinguish between the species. Nevertheless, I suggest that in future identifications of these three species, details of individual specimen measurements may possibly benefit the eventual solution of this species-complex. To summarize, *D. achlora*, *D. gramen* and *D. lobostoma* can be identified by size and detailed knowledge of the shell structure (i.e. number of pores surrounding the aperture and the size of the mesh in the organic network).

In the other ovoid species described here, *D. tuberculata* and *D. wailesi*, the evidence put forward to distinguish between them is also based on differences of shell structure. Specimens of *D. tuberculata* have the typical protuberances which are usually pronounced or sometimes slightly flattened, but in either case they are frequently represented by aggregates of small particles. Such aggregates are present in specimens constructed of either quartz particles or diatom frustules. *D. wailesi* by contrast has a smooth shell composed mainly of diatom frustules, with the shell components arranged irregularly, and there are no aggregates of small particles. Whilst there is a slight difference between the two species in the number of indentations surrounding the apertural opening, no particular significance is

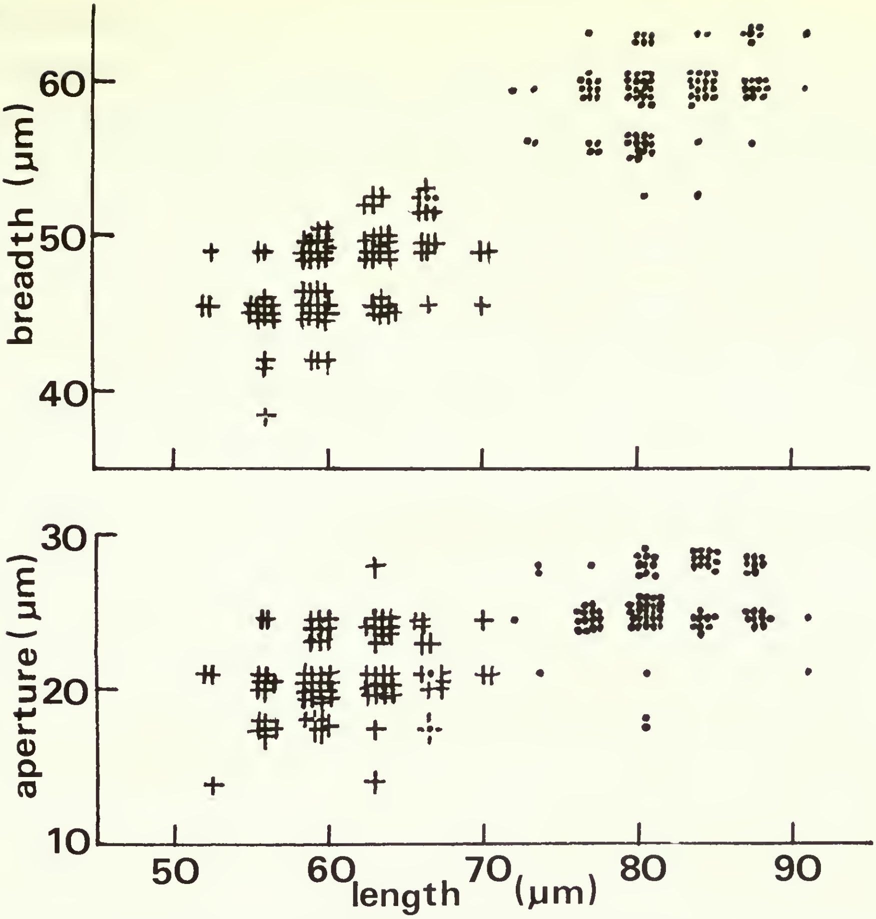


Fig. 31 Plot of individual measurements for specimens of *Difflugia achlora* (crosses) and *D. gramen* (points) taken from Stepánek & Jiri (1958)—breadth (upper) and diameter of aperture (lower) vertical axis; total shell length, horizontal axis.

attached to this feature at present, especially as the depth of the indentations varies in each specimen which suggests that this may be an unreliable character. There are slight differences in size between the two species, but the data is too sparse to be useful.

Our observations on pyriform species of *Difflugia* show that the structure and appearance of the shell have so far been reliable diagnostic characters. The ability of *D. tuberculata* to construct a similar shell of either quartz or diatom frustules would seem to strengthen this argument. Especially as there is no similar evidence of this ability in pyriform species, which tend to be more conservative in their choice of construction material. I therefore consider that the difference between the shells of *D. tuberculata* and *D. wailesi* is a sufficiently strong character to distinguish between these two ovoid species.

In conclusion, it is fair to say that the examination of these five ovoid species of *Difflugia* has shown how difficult it is to establish good diagnostic characters in these forms than it is in pyriform species.

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The genus *Azygocypridina* Sylvester-Bradley (Crustacea : Ostracoda) with particular reference to *A. imperialis* (Stebbing, 1901)

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Introduction

This is the first paper in which the adults and juveniles of both sexes of a species of *Azygocypridina* have been described and illustrated together. Previous descriptions of new species have usually been based upon single specimens. Consequently, although nine species of *Azygocypridina* have been described, we still know very little about the genus, and it has not been clear which morphological features characterize individual species or which indicate a particular instar or sex.

One hundred and three specimens of *Azygocypridina imperialis* (Stebbing) were collected during cruises of R.R.S. *Discovery* and R.R.S. *Challenger* in 1971, 1974, 1976, 1978 and 1979 at stations in the N.E. Atlantic (see Table 1). The specimens included both adults and immature instars and were obtained from depths between 1950 m and 2930 m mainly by means of an epibenthic sledge (see Aldred *et al.*, 1976).

Systematic descriptions

Sub-class OSTRACODA Latreille, 1802 (*nom. correct.*, Latreille, 1806)
Order **MYODOCOPIDA** Sars, 1866
Sub-order **MYODOCOPINA** Sars, 1866
Family **CYPRIDINIDAE** Baird, 1850
Sub-family **AZYGOCYPRIDININAE** Kornicker, 1970 (*nom. nov.* for Crossophorinae Skogsberg, 1920)
Genus *AZYGOCYPRIDINA* Sylvester-Bradley, 1950

TYPE SPECIES: (by monotypy) *Crossophorus imperator* Brady, 1880

Crossophorus Brady, 1880 : 158
Crossophorus Brady; Brady and Norman, 1896 : 643
Crossophorus Brady; Müller, 1906*a* : 133 (*non Crossophorus* Hemprich & Ehrenberg, 1828—a nematode—senior homonym)
Azygocypridina Sylvester-Bradley, 1950 : 364 (*pro Crossophorus* Brady, 1880)

DIAGNOSIS. Adult: carapace robust, large (4–15·5 mm), ovate/globular with small rostrum and incisure; no caudal process; margins smoothly rounded; ornament lacking except for minute punctae. Outer lobe of third podomere of fifth limb exopodite bears two setae. 'Minor' spines of furcal lamellae more than half the length of the adjacent 'major' spines.

In male: endopodite of second antenna reflexed; *b*-seta and *c*-seta of first antenna with spoon-like setules.

SPECIFIC DETERMINATION IN *AZYGOCYPRIDINA*. Table 2 summarizes all the published records of species of *Azygocypridina*. With the exception of *A. imperialis* (Stebbing) and *A.*

Bull. Br. Mus. nat. Hist. (Zool.) **39** (3) : 139–160 Issued 27 November 1980

Table 1 Sampling data for collections of *Azygocypridina imperialis.*

Research Vessel	Cruise No.	Station and Haul No.	Position lat. long.	Depth (m)	Gear	Date
Discovery	39	7709#62	60°N 20°W	2714	sledge*	1.5.1971
Discovery	39	7709#73	60°N 20°W	2633–2646	sledge*	5.5.1971
Discovery	39	7709#85	60°N 20°W	2708	sledge*	7.5.1971
Discovery	39	7711#57	53°N 20°W	2656–2658	sledge*	27.5.1971
Discovery	39	7711#58	53°N 20°W	2615–2621	sledge*	27.5.1971
Discovery	61	8511#1	42°N 11°W	2384–2399	sledge*	5.5.1974
Discovery	61	8512#4	42°N 11°W	2281–2465	sledge*	7.5.1974
Discovery	61	8514#1	42°N 11°W	2622–2632	sledge*	8.5.1974
Discovery	79	9133#5	21°N 18°W	2112–2160	sledge*	25.11.1976
Discovery	79	9133#7	21°N 18°W	2130–2191	otter trawl	26.11.1976
Discovery	79	9134#0	21°N 18°W	1949–1942	sledge*	26.11.1976
Discovery	92	9753#7	51°N 12°W	1942	sledge*	8.4.1978
Challenger	9/79	50605#1	50°N 13°W	2820–2930	sledge*	5.7.1979

*For a complete description of epibenthic sledge see Aldred *et al.*, 1976.

africanus (Stebbing), the descriptions of all these species have been based on single specimens. Differences in the terminal part of the seventh limb and in the number of furcal spines were used by Stebbing (1901) to distinguish *A. imperialis* from *A. imperator* (Brady) and *A. africanus*. Granata (1919) also used numbers of furcal spines, as well as carapace size, to distinguish between *A. grimaldii* (Granata) (= *A. imperialis*), *A. imperator*, *A. gibber* (Müller) and *A. africanus*. Both Müller (1912) and Rudjakov (1961) used the number of setae on the seventh limb to separate species of *Azygocypridina*. McKenzie (1968) used this character, together with shape, to establish a new species which he did not formally name.

Of the characters used for specific determination by earlier authors, the number of furcal spines can be disregarded as being of no taxonomic importance at the specific level in *Azygocypridina*. A comparison of the furcal lamellae from eight adult specimens of *A. imperialis* showed that there can be considerable variation in the numbers and arrangement of spines within a single species, and often between the two furcal lamellae of the same individual (see Table 3). An examination of several specimens of *A. imperialis* showed that, generally, the number of furcal spines increases from eight in the A-5 instar to a maximum of twenty-nine in some adults, presumably by interpolation of 'minor' spines between the 'major' spines at each moult. In Table 3 the numbers in the first column indicate the position, in sequence from the distal end, of the 'major' spines amongst the 'minor' spines. 'Major' and 'minor' spines are distinguished subjectively; the 'major' spines are conspicuously stouter and longer than the 'minor' spines. Where it has been difficult to decide whether spines are 'major' or 'minor', the numbers are shown in brackets.

Table 2 Summary of published records of *Azygocypridina* spp.

Species	Sex	Length	Height	Group	Locality	Depth (m)	Temp °C	Substrate	No. of specimens	Reference
A. imperator (Brady)	♂	8·4	—	I	S. Pacific	2012	2	grey ooze	I ♂	Brady, 1880
A. africanus (Stebbing)	♀	11·25–15·5	8·75–13·0	I	S. Africa	165–229	~5	rough bottom with sand and shells	♀♀ and juvenile	Stebbing, 1901, 1902
A. africanus (Stebbing)	♀	11·0	8·75	I	S. Africa	156	—	—	♀ and juveniles	Müller, 1906*a*,*b*
A. gibber (Müller)	♂	4·0	—	II	Indonesia	1158	—	grey mud with brown liquid surface	1 ♂	Müller, 1906*b*
A. birnsteini Rudjakov	♀	9·1	—	II	N. Pacific	1050–1070	—	—	1 ♀	Rudjakov, 1961
A. sp. Rudjakov	♂	7·5	—	II	N. Pacific	1050–1070	—	—	1 ♂ juvenile	Rudjakov, 1961
A. sp. Kornicker	♀	8·8*	—	—	N. Pacific	850	3·3	brown mud	1 ovigerous ♀	Kornicker, 1969
A. rudjakovi Kornicker	♂	10·1	9·0	III	S. Pacific	1411–1450	~3	—	1 ♂	Kornicker, 1970
A. sp. McKenzie	♀	11·0	7·5	I	Tasman Sea	180	—	—	1 ovigerous ♀	McKenzie, 1968
A. imperialis (Stebbing)	♀	7·0	—	I	N. Atlantic	2633	2·8	—	1 ♀ juvenile	Brady & Norman, 1896
A. grimaldii (Granata) (= *A. imperialis*)	♂	8·0	6·5	I	N. Atlantic	2320	—	—	1 ♂	Granata, 1919; Granata & Caporiacco, 1949
A. imperialis (Stebbing)	♀	8·33–10·13	7·33–8·7	I	N. Atlantic	1942–2714	—	foraminiferal ooze	103 adult and juvenile ♂♂ & ♀♀	herein
	♂	6·84–8·16	5·8–6·8	I						

*not 2·2 mm as stated in Kornicker (1969), caption to fig. 9 (pers. comm., Kornicker, 1980).

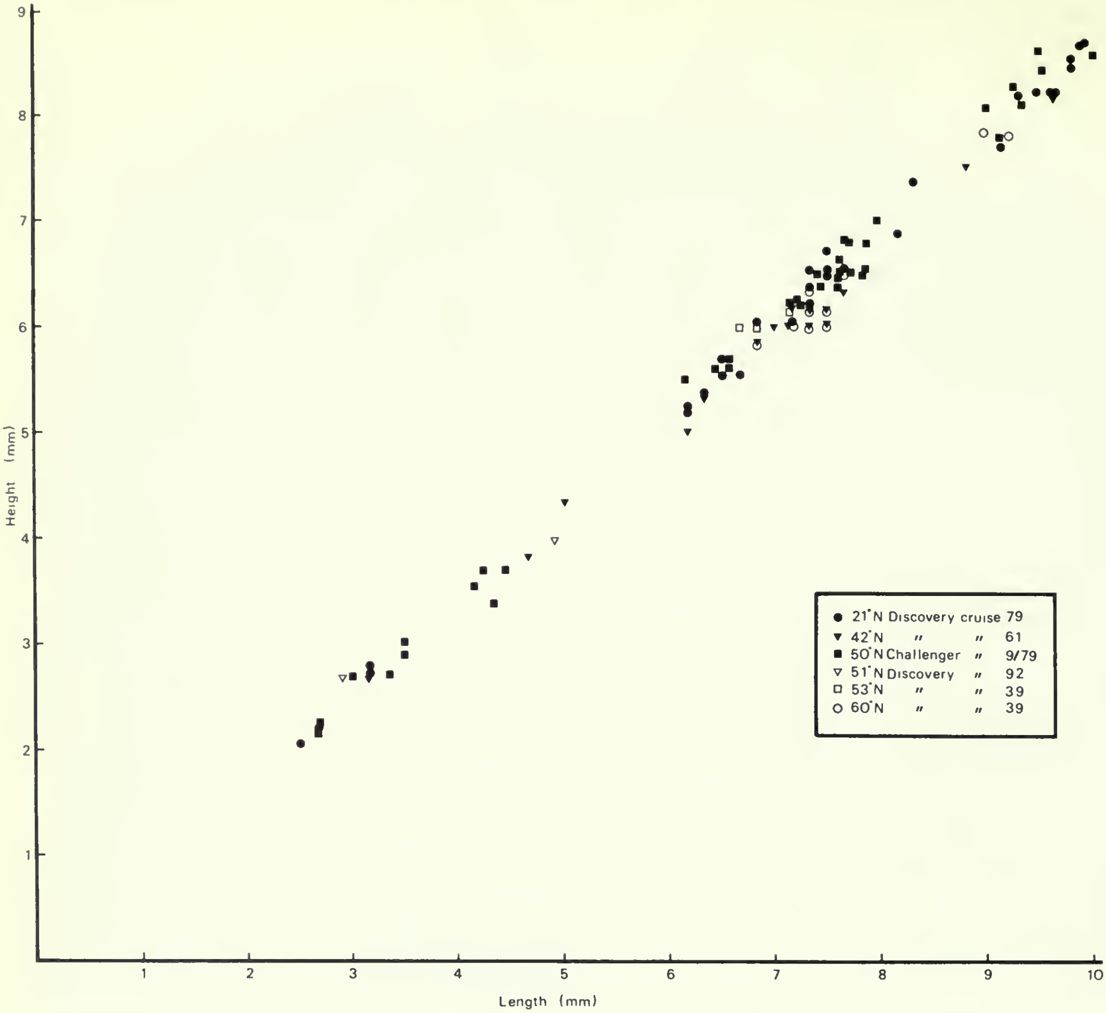

Fig. 1a Size distribution of *Azygocypridina imperialis* (Stebbing) from the N.E. Atlantic.

Müller (1912) considered the number of marginal setae on the seventh limb to be a character of major diagnostic importance, and he recognized three species on this basis. He stated that *A. imperator* had twenty marginal setae, this number being derived from the original description of a single specimen by Brady & Norman (1896). The specimen they examined, however, was subsequently recognized as being distinct from *A. imperator s.s.*, was renamed *A. imperialis* by Stebbing (1901), and is shown herein to be A-2♀ instar. An examination of several adult specimens of *A. imperialis* showed that the male bears about forty setae, and the female about sixty setae, marginally. Müller (1912) also stated that *A. africanus* (female) bore one-hundred marginal setae. However, a single female specimen of this species examined by the present author was found to have about three times this number of setae. Müller (1906*b*, 1912) reported finding sixty setae in *A. gibber* (male), and McKenzie (1967) found about three hundred setae in his *A.* sp. (female). These inconsistencies suggest that specific diagnoses of *Azygocypridina* based solely upon the number of setae on the seventh limb are open to doubt.

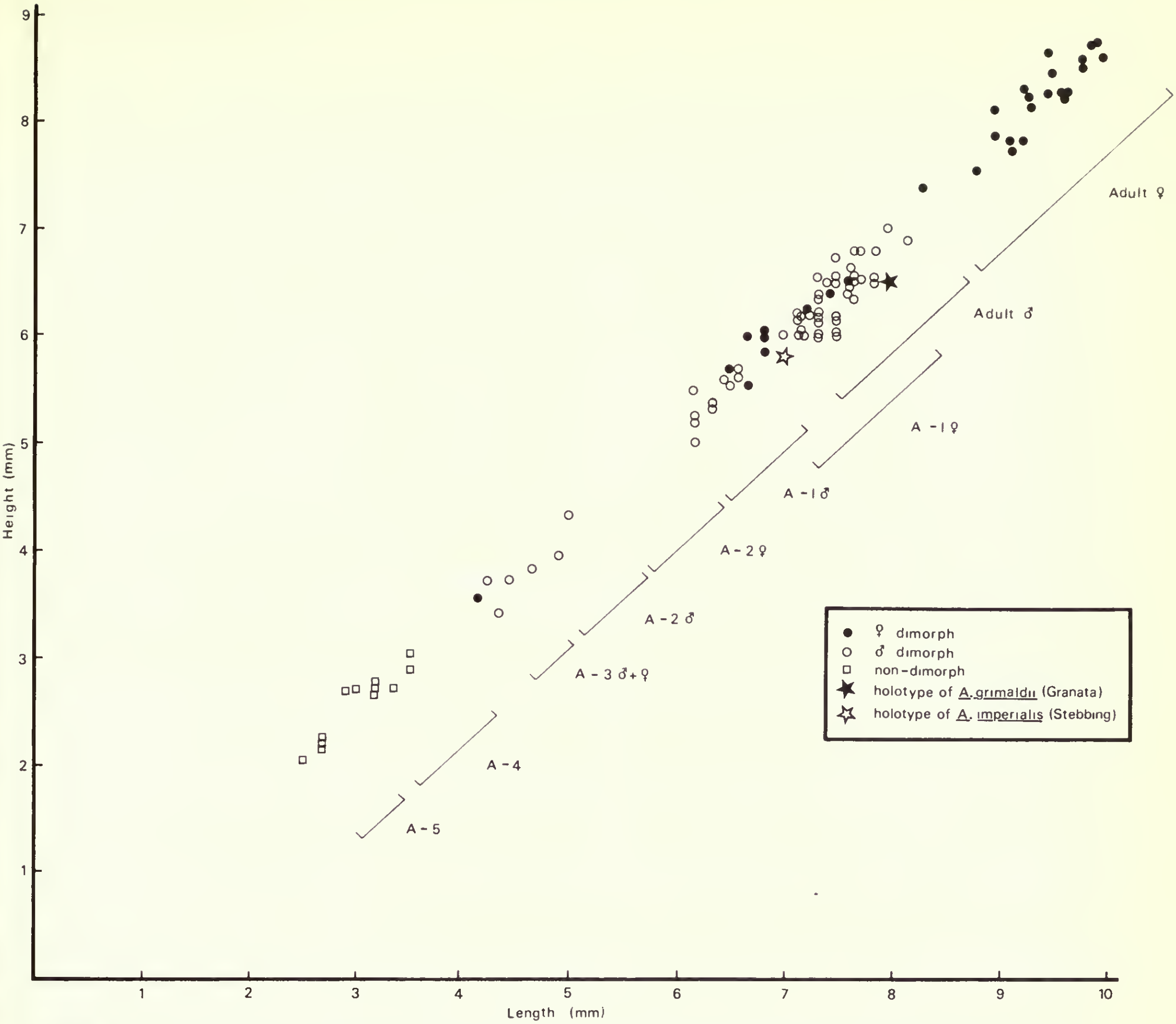

Fig. 1b Ontogenetic sequence of *Azygocypridina imperialis* (Stebbing) from the N.E. Atlantic. The sizes of the holotypes of *A. imperialis* and *A. grimaldii* (Granata) are included for comparison.

Kornicker (1970) arranged all the known species into three groups based on the morphology of the terminal part of the seventh limb (see Table 2). In *A. imperialis* the male and female seventh limbs terminate in markedly different structures (see Figs 6B, D-F). Both sexes do fit into Kornicker's Group I, but care should be taken in using this character in classification until both sexes of the species being determined are known.

Size and shape of the carapace are considered to be poor specific characters for most species. Exceptions are *A.* sp. of McKenzie (1968) which is distinctively ovate and *A. africanus* which is the largest species yet discovered. It may be possible to recognize *A. gibber* by its small size (about 4·00 mm long) but in all other species neither size nor shape is sufficiently distinctive to be of use at the specific level of diagnosis. No relationship seems to exist between water depth and size or shape, but each known species appears to have a distinct geographical range.

Table 3 Distribution of 'major' and 'minor' furcal spines in eleven specimens of *Azygocypridina imperialis*.

The numbers indicate the position, in sequence from the distal end, of the 'major' spines amongst the 'minor' spines. Where it has not been possible to decide whether spines are 'major' or 'minor', the numbers are shown in brackets.

Position of 'major' spines	Total number of furcal setae	Sex and instar	Station and Haul Nos.
L 1 2 5 8 12 15 17	26	A♂	7709#85
R 1 2 6 9 12 14 16 18 20	27		
L 1 2 5 (6) 9 12 14 18	24	A♂	8511#1
R 1 2 5 9 12 14 16 18	24		
L 1 2 5 8 11 14 16	23	A♂	7709#73
R 1 2 5 8 11 13	23		
L 1 2 5 8 11 13 15	24	A♂	7709#73
R 1 2 5 8 11 14 16	24		
L 1 2 (3) 6 10 13 16 (18)	26	A♂	7709#73
R 1 2 6 10 14 17 19	28		
L 1 2 6 9 12 14	22	A♂	7709#73
R 1 2 6 10 13 15	24		
L 1 2 5 8 11 13 15	22	A♂	7709#73
R 1 2 5 (6) 8 10 12 14 16	22		
L 1 2 6 8 10 13 16 18	25	A♀	8511#1
R 1 2 6 8 11 15 18 20 (22)	29		
L 1 2 5 8 12 15 (17)	24	A–1♂	8511#1
R 1 2 6 9 12 15 (17)	22		
L 1 2 (3) 5 7 9 11	16	A–2♂	8514#1
R 1 2 5 7 9 11	18		
L 1 2 3 4 5 6 7 8	8	A–3♀	8514#1
R 1 2 3 4 5 6 7 8	8		

Azygocypridina africanus (Stebbing), 1901

Crossophorus africanus Stebbing, 1901 : 100 (no illustration)
Crossophorus africanus Stebbing: Stebbing, 1902 : 79; pls 15a, 16.
Crossophorus africanus Stebbing; Müller, 1906*a* : 134; pl. 34, figs 1–9.
Azygocypridina africanus (Stebbing), Sylvester-Bradley, 1950 : 364 (new combination).

LECTOTYPE. (designated herein). A female carapace (15·0 mm long) and appendages. Brit. Mus. (Nat. Hist.) No. 1928. 12.13064.

TYPE LOCALITY. Mosselbaai, S. Africa, approx. lat. 34°12′S, long. 22°08′E; collected by a Dr Gilchrist aboard the *Peter Faure*; depth 90–100 fms (164–182 m).

DISTRIBUTION. S. Africa (Stebbing, 1901, 1902; Müller, 1906*a*); found at depths of between 156 m and 229 m; temperature about 5°C; associated with a rough substrate of sand and shells.

DIAGNOSIS. Characteristic setal complement of first and second antennae (see Fig. 2). Seventh limb of the adult female bears about 300 setae marginally and terminates in an inflated tip, divided into two opposing 'jaws', one of which terminates in a group of about 10 teeth, the other in a single hooked 'tooth'. Each 'jaw' bears a cluster of 30–40 setae. Length : height : breadth ratio of adult female carapace is about 100 : 86 : 54. Adult male unknown.

Table 4 Mean carapace dimensions of adults and A – 1 instars of *A. imperialis* and *A. africanus* (see p. 156).

Number of Specimens	Species	Sex	Length	Height	Breadth
28	*A. imperialis*	♂	7·3 (100)	6·2 (82)	4·25 (67)
13	*A. imperialis*	♀	9·5 (100)	8·0 (85)	6·1 (64·5)
5	*A. imperialis*	A–1♂	6·23 (100)	5·2 (83·5)	4·0 (64)
4	*A. imperialis*	A–1♀	6·63 (100)	5·66 (85·4)	4·33 (65·3)
1	*A. africanus*	♀	15·0 (100)	12·9 (86)	8·1 (54)
1	*A. africanus*	A–1♂	10·8 (100)	9·18 (85)	6·37 (59)

Azygocypridina imperialis (Stebbing), 1901
(Figs 4–11)

Crossophorus imperator Brady; Brady & Norman, 1896 : 643, pl. 53, figs 1–11. (*non C. imperator* Brady, 1880 : 158)
Crossophorus imperialis Stebbing, 1901 : 100.
Crossophorus grimaldii Granata, 1919 : 1, text–figs 1–7.
Crossophorus grimaldii Granata; Granata & Caporiacco, 1949 : 5; pl. 1, fig. 1; pl. 2, figs 1–12.
Azygocypridina imperialis (Stebbing); Sylvester-Bradley, 1950 : 364 (new combination).

HOLOTYPE. Female juvenile (A-2 instar); appendages and carapace fragments: B.M.(N.H.) 1911.11.8.3901, 1911.11.8.36759.

TYPE LOCALITY. 'Porcupine' station no. 20 (approx. lat. 55°11′N, long. 11°31′W); depth 1443 fathoms (2639 m); temperature 2·8°C, date 1869.

DISTRIBUTION. N.E. Atlantic, 1900–2930 m, associated with foraminiferal ooze.

REMARKS. In 1919, Granata introduced *Crossophorus grimaldii* as a new species, based on a single adult male specimen from the N.E. Atlantic. The original description was brief and accompanied by a few poor illustrations. Granata and Caporiacco, 1949, reillustrated the same specimen, which by this time had been lost. Comparison of these latter illustrations with my own specimens strongly suggests that *C. grimaldii* is identical to and, therefore, a junior synonym of, *A. imperialis*. Moreover, Granata's specimen was collected from the same geographical area as the '*Discovery*' and '*Challenger*' material.

DIAGNOSIS. Adult; characteristic setal complement of the first and second antennae (see Fig. 2). Seventh limb of male has about forty marginal setae and terminates in paired 'jaws', each with a cluster of about ten setae. One 'jaw' bears three stout 'teeth', the other a single hooked 'tooth'. Seventh limb of female has about sixty marginal setae and terminates in two opposing 'jaws', one with three 'teeth', the other with a large hooked 'tooth' and about eight short 'teeth'. Length : height : breadth ratio of ♂, 100 : 82 : 67; of ♀, 100 : 85 : 64. Carapace almost circular in lateral view, highly inflated, with no obvious ornamentation; surface finely punctate and bearing rimmed pores, some with, and others without, marginal protuberances. Rostrum small, acuminate; incisure parallel-sided, moderately deep. Muscle scar pattern consists of five more-or-less vertically elongate scars in a horizontal row, with a

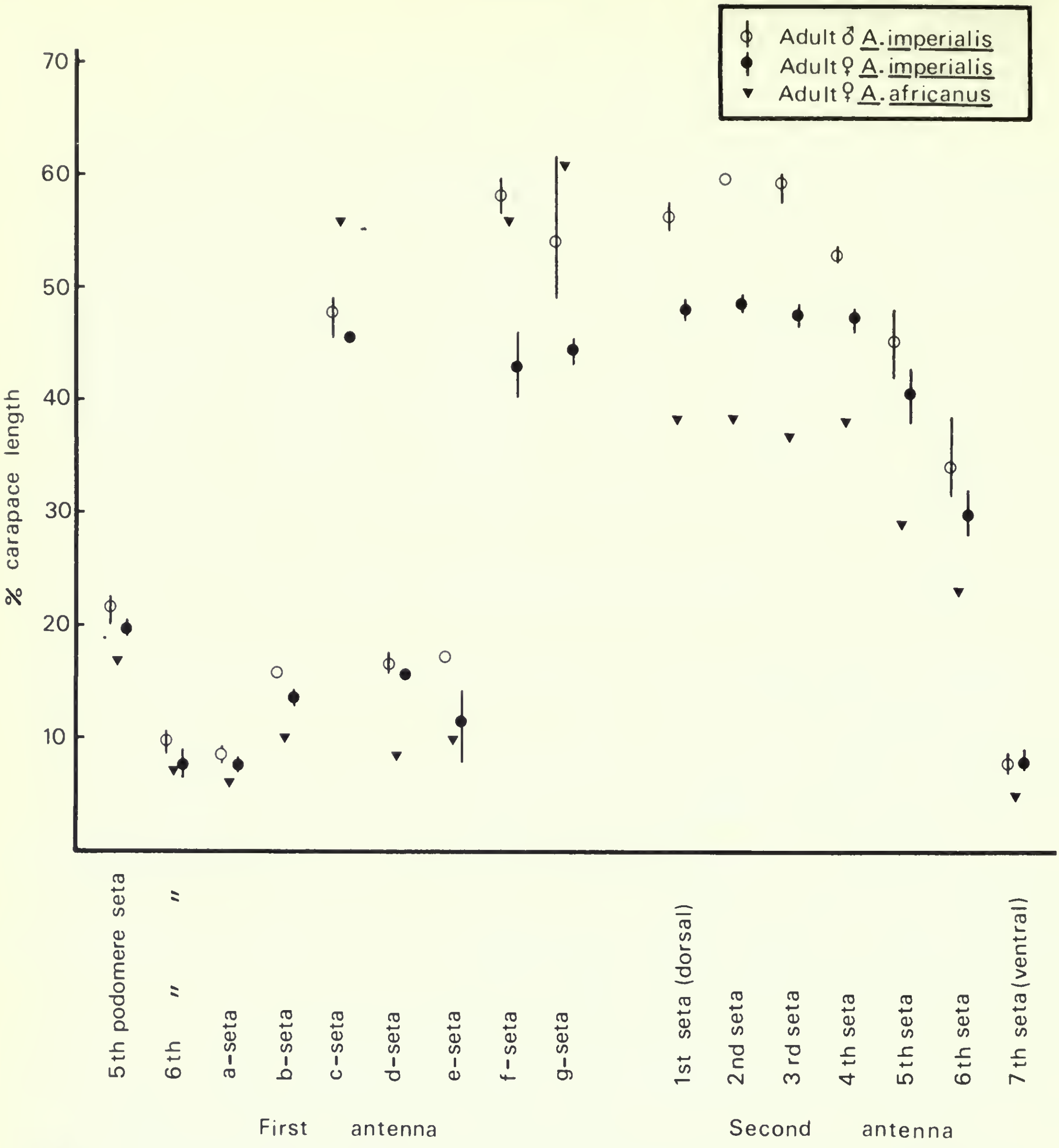

Fig. 2 Comparison of the meristic characters of the 1st and 2nd antennae of adult specimens of *A. imperialis* and *A. africanus*.
The mean lengths of setae from the left and right appendages of two specimens of *A. imperialis* are shown together with their observed ranges. These values are compared with measurements from a single adult female of *A. africanus*. All measurements are expressed as percentages of the mean carapace length.

curved cluster of eight or nine round/slightly elongate scars posteriorly; U-shaped anterior muscle scar. Freshly caught specimens observed in the net have orange soft parts and milky-white translucent carapaces (Angel, pers. comm.). With back lighting in the laboratory they appear to have red bodies whilst the carapaces are tinted purple.

Appendages of adult *A. imperialis*

Examination of appendages from several specimens of both sexes showed that the number of

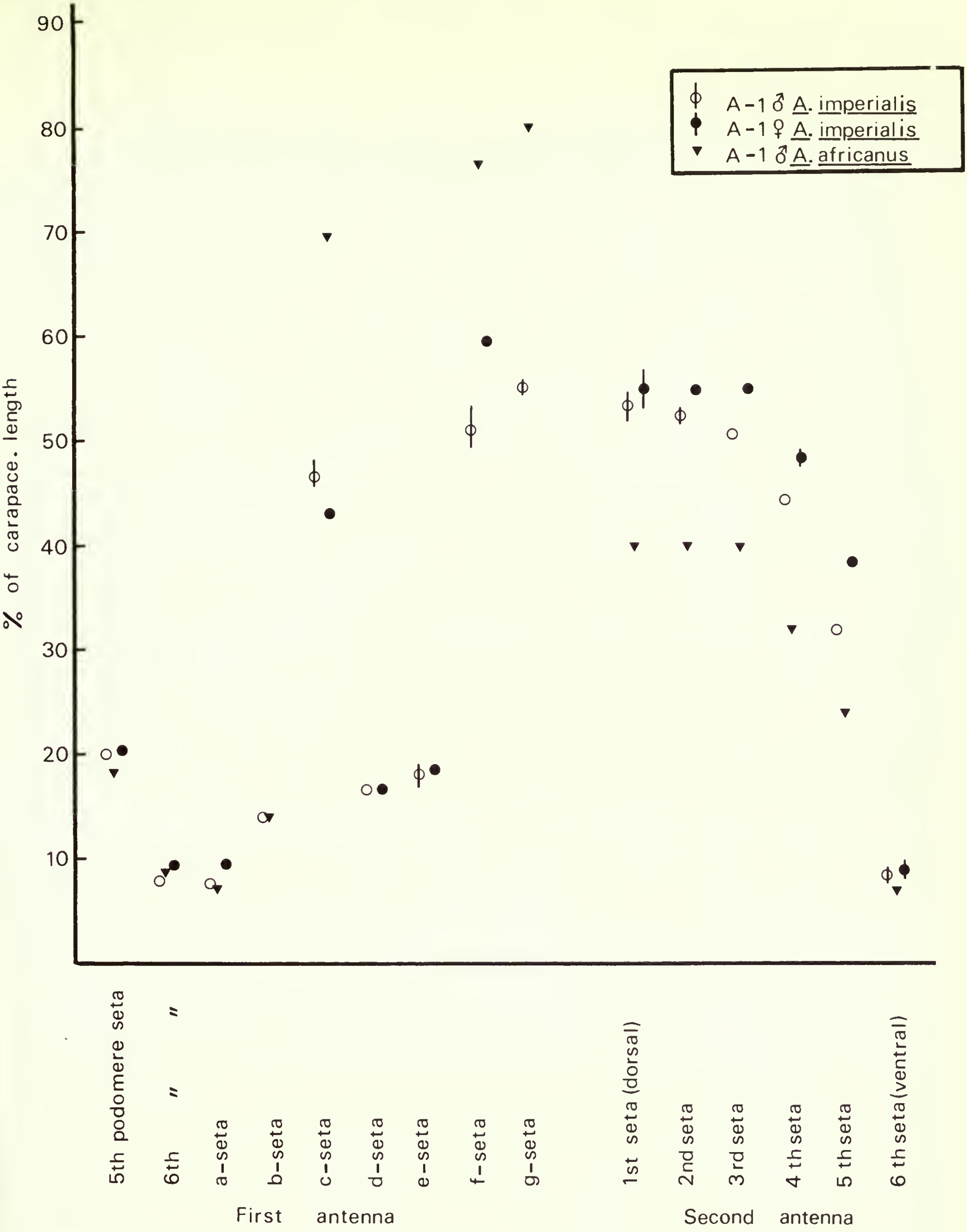

Fig. 3 Comparison of the meristic characters of the 1st and 2nd antennae of A-1 instars of *A. imperialis* and *A. africanus*.
The mean lengths of setae from the left and right appendages of two specimens of *A. imperialis* are shown together with their observed ranges. These values are compared with measurements from a single A-1 male of *A. africanus*. All measurements are expressed as percentages of the mean carapace length. (Data incomplete for both species.)

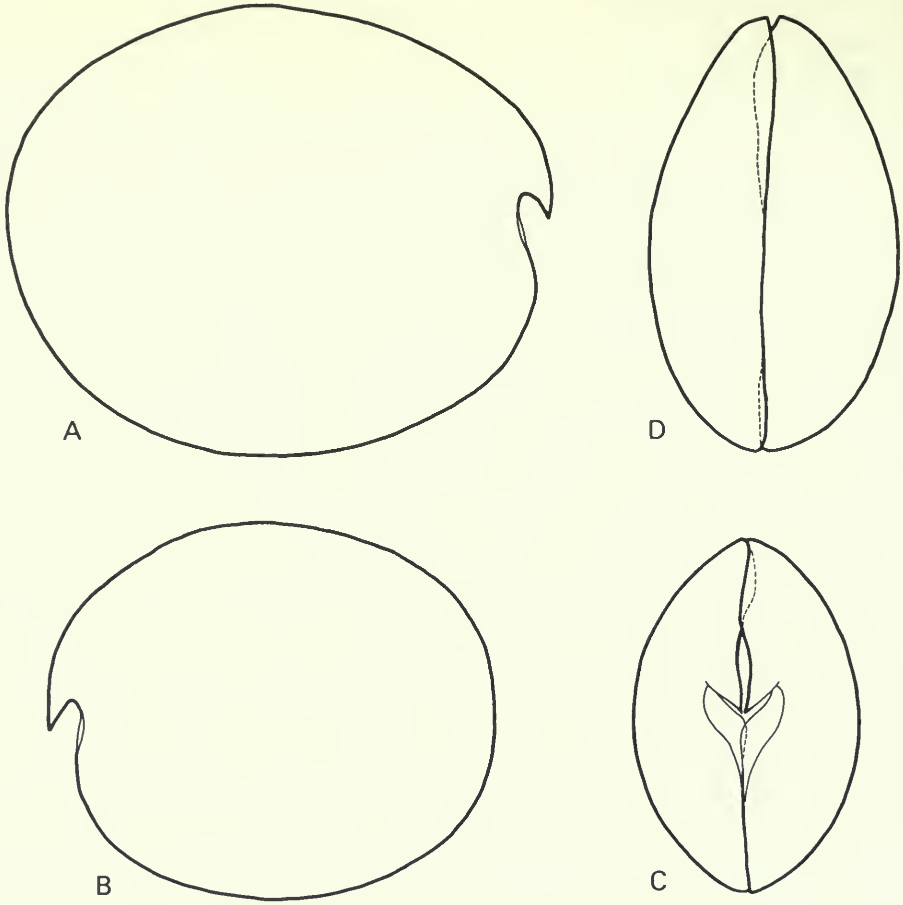

Fig. 4 *Azygocypridina imperialis* (Stebbing). A-D carapace profiles: A, female, right valve, external; B, male, left valve, external; C, male, carapace, anterior; D, male, carapace, dorsal.

small setae varied from one individual to another and, sometimes, between left and right appendages of the same individual. Table 3 shows the individual variations in the setal complement of the furcae. In other appendages variation in setation may have resulted from loss of setae during the preparation of specimens for examination. In general, differences in the setal complement of appendages are not an expression of sexual dimorphism in *A. imperialis*. Obvious exceptions to this are to be found in the first and second antennae, and in the seventh limb. (See section on Ontogeny and Sexual Dimorphism.)

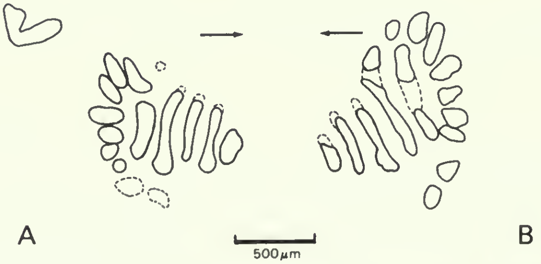

Fig. 5 *Azygocypridina imperialis* (Stebbing). Muscle scar patterns: A, female, left valve internal; B, male, right valve internal. Arrows point anteriorly.

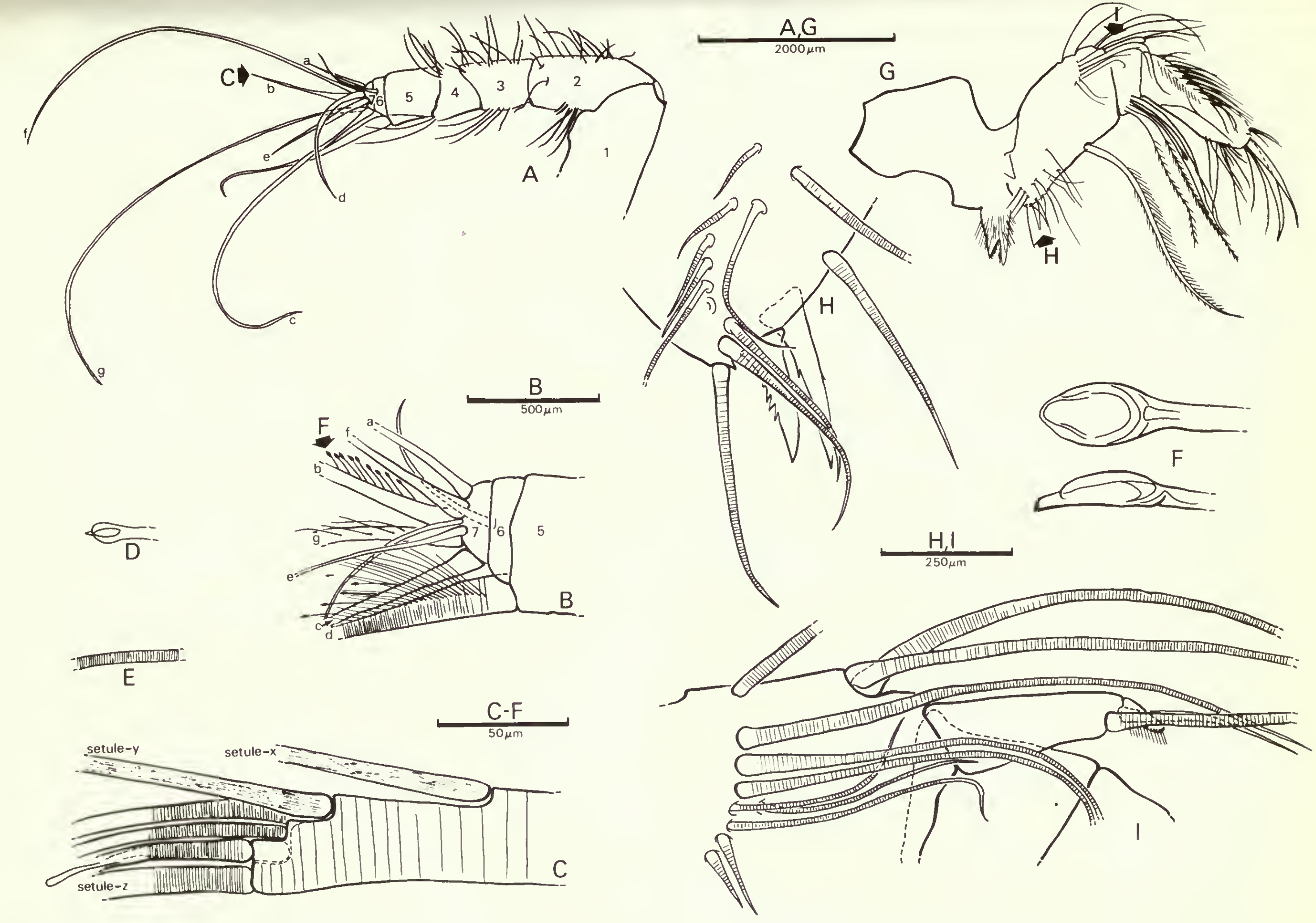
A,G
2000μm
A
a
b
c
d
e
f
g
1
2
3
4
5
6
7
C
G
H
I
B
500μm
F
D
E
C-F
50μm
setule-y
setule-x
setule-z
H,I
250μm

Fig. 6 *Azygocypridina imperialis* (Stebbing)
A-F: male, first antenna B.M.(N.H.) 1979.231
A: whole appendage
B: details of setae borne on podomeres 5–7
C: tip of *b*-seta
D: tip of setules 'x' and 'y' of *b*-seta
E: tip of setule 'z' of *b*-seta
F: tip of spoon-like setules of *b*-seta
G-I: female, mandible B.M.(N.H.) 1979.232
G: whole appendage
H: details of ventroproximal part of basale
I: details of dorsodistal part of basale

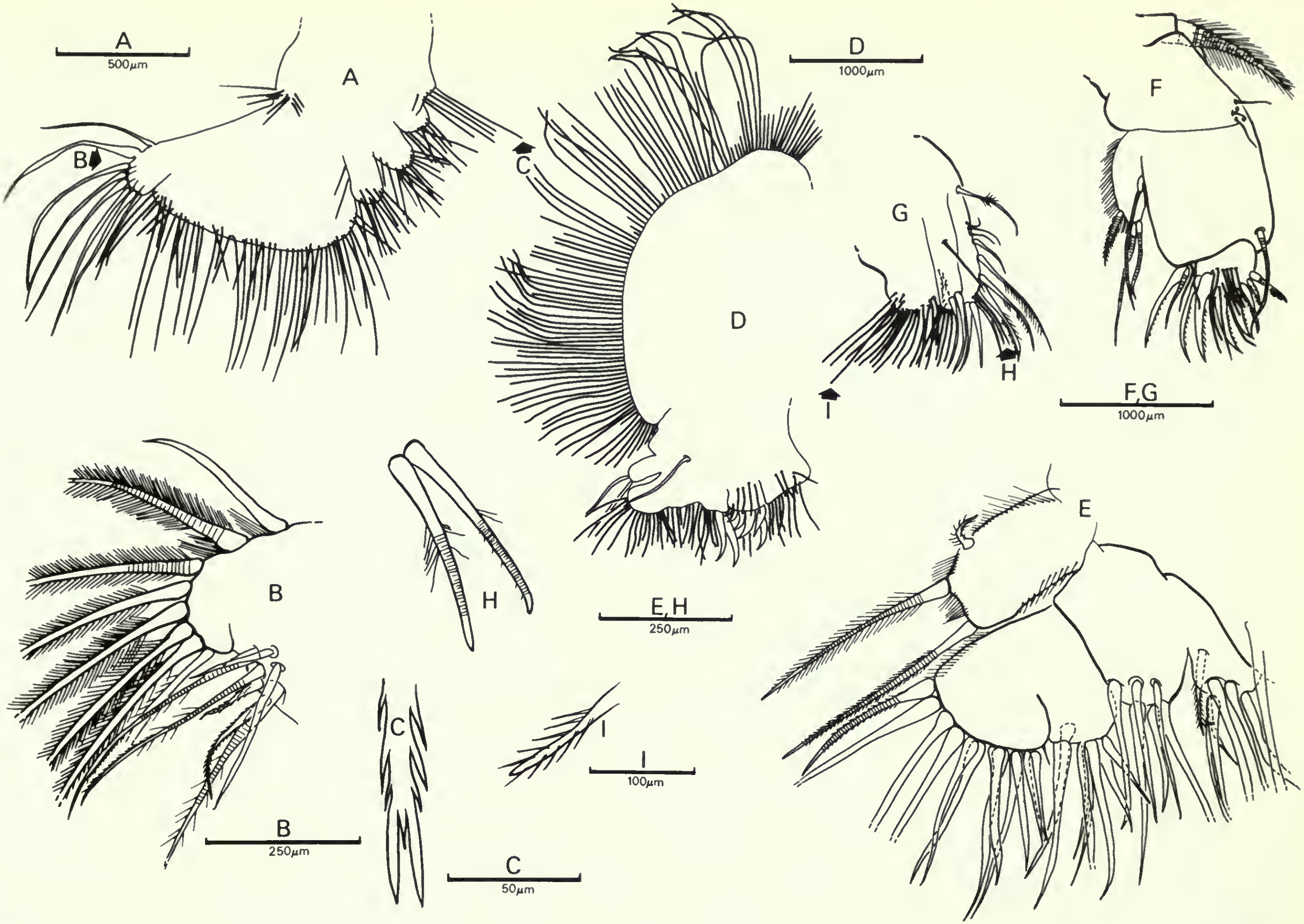
A
500μm
A
B
C
D
1000μm
D
G
H
I
F
F,G
1000μm
B
H
E,H
250μm
E
C
I
I
100μm
B
250μm
C
50μm

Fig. 7 *Azygocypridina imperialis* (Stebbing)
A-C: sixth limb, male. B.M.(N.H.) 1979.233
A: whole appendage
B: details of terminal podomere
C: tip of triaenid seta of 'A'
D: female, fifth limb, whole appendage B.M.(N.H.) 1979.234
E: male, fifth limb, details of exopodite B.M.(N.H.) 1979.233
F-I: male maxilla B.M.(N.H.) 1979.231
F: limb without endites
G: endites
H: setae from 'G'
I: seta from 'G'

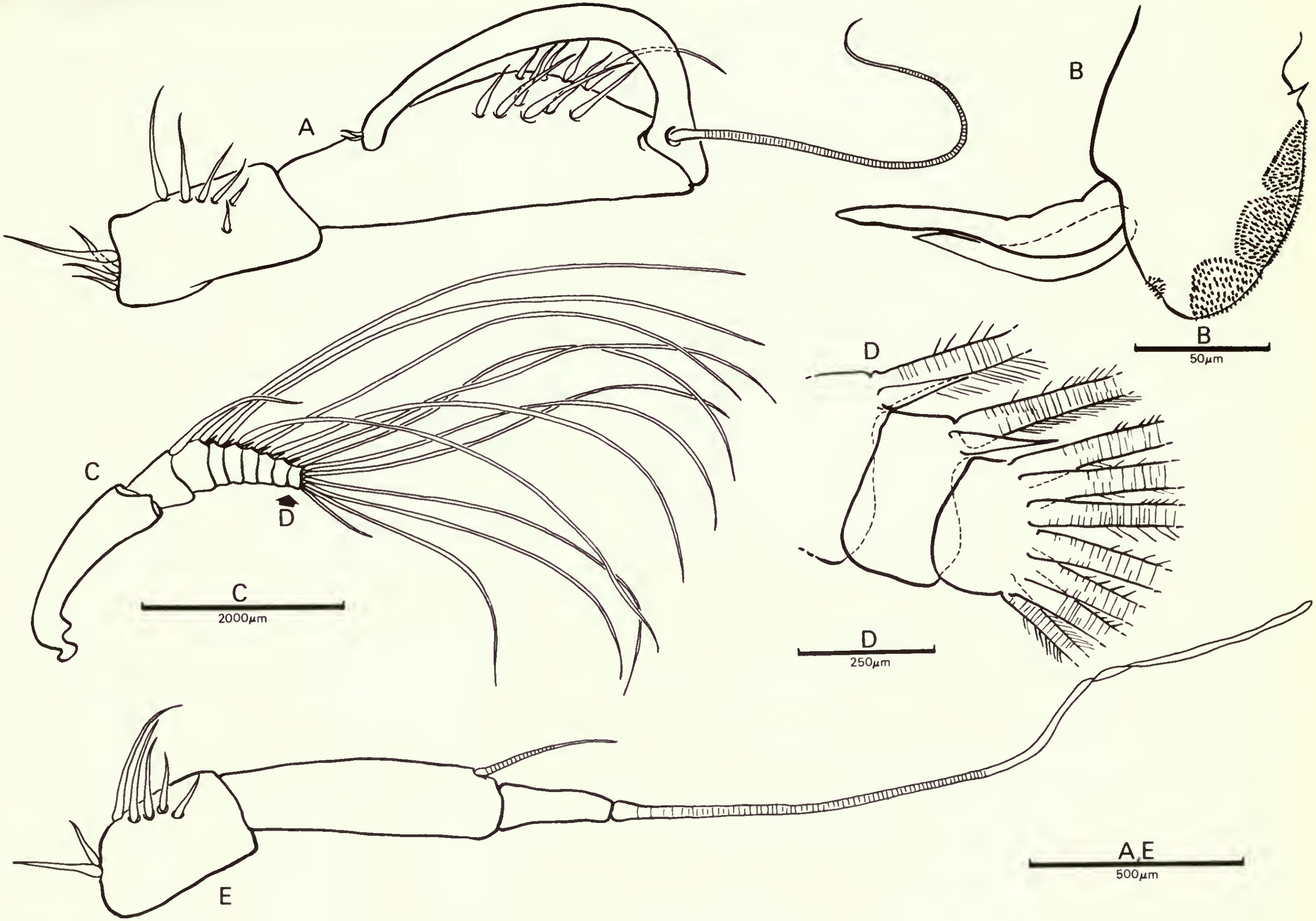
A
B
B
50µm
C
D
C
2000µm
D
D
250µm
E
A,E
500µm

Fig. 8 *Azygocypridina imperialis* (Stebbing)
A, B: male second antenna B.M.(N.H.) 1979.233
A: endopodite
B: detail of tip of third podomere of endopodite
C-E: female second antenna B.M.(N.H.) 1979.232
C: exopodite
D: detail of podomeres 7–9 of exopodite
E: endopodite

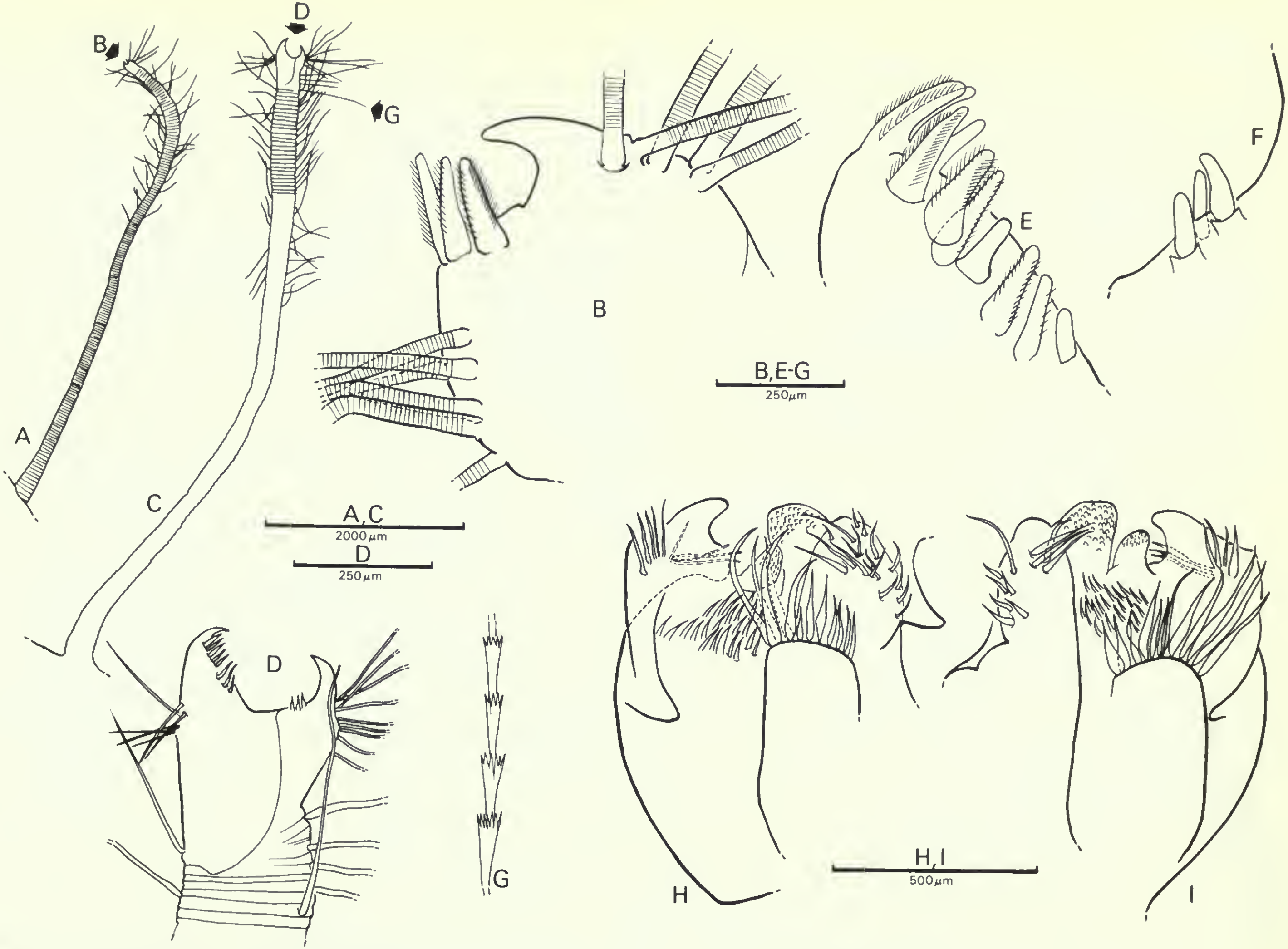
B
D
G
A
C
B
E
F
B,E-G
250μm
A,C
2000μm
D
250μm
D
G
H,I
500μm
H
I

Fig. 9 *Azygocypridina imperialis* (Stebbing)
A, B: male, seventh limb B.M.(N.H.) 1979.231
A: whole appendage
B: detail of tip of 'A'
C-G: female, seventh limb B.M.(N.H.)1979.232
C: whole appendage
D: detail of tip of 'C'
E, F: detail of tip of 'D'
G: bell-shaped seta from 'C'
H, I: male, copulatory appendages B.M.(N.H.) 1979.233

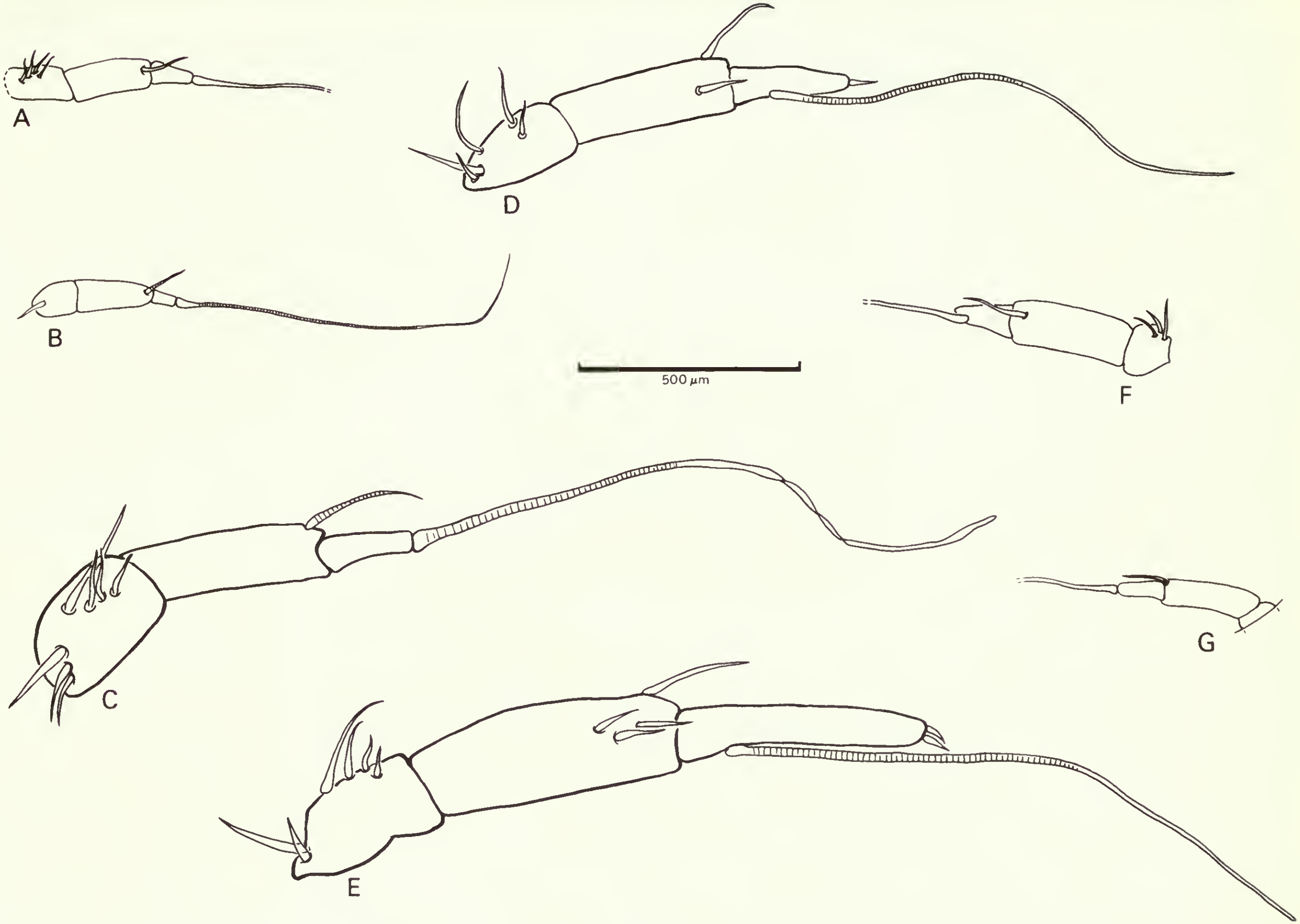

Fig. 10 *Azygocypridina imperialis* (Stebbing)
A-G: juveniles, endopodite of second antenna
A: female A-2 (holotype) B.M.(N..H.) 1911.11.8.3901
B: female A-3 B.M.(N.H.) 1979.235
C: female A-1 B.M.(N.H.) 1979.236
D: male A-2 B.M.(N.H.) 1979.237
E: male A-1 B.M.(N.H.) 1979.238
F: male A-3 B.M.(N.H.) 1979.434
G: A-4 B.M.(N.H.) 1979.435

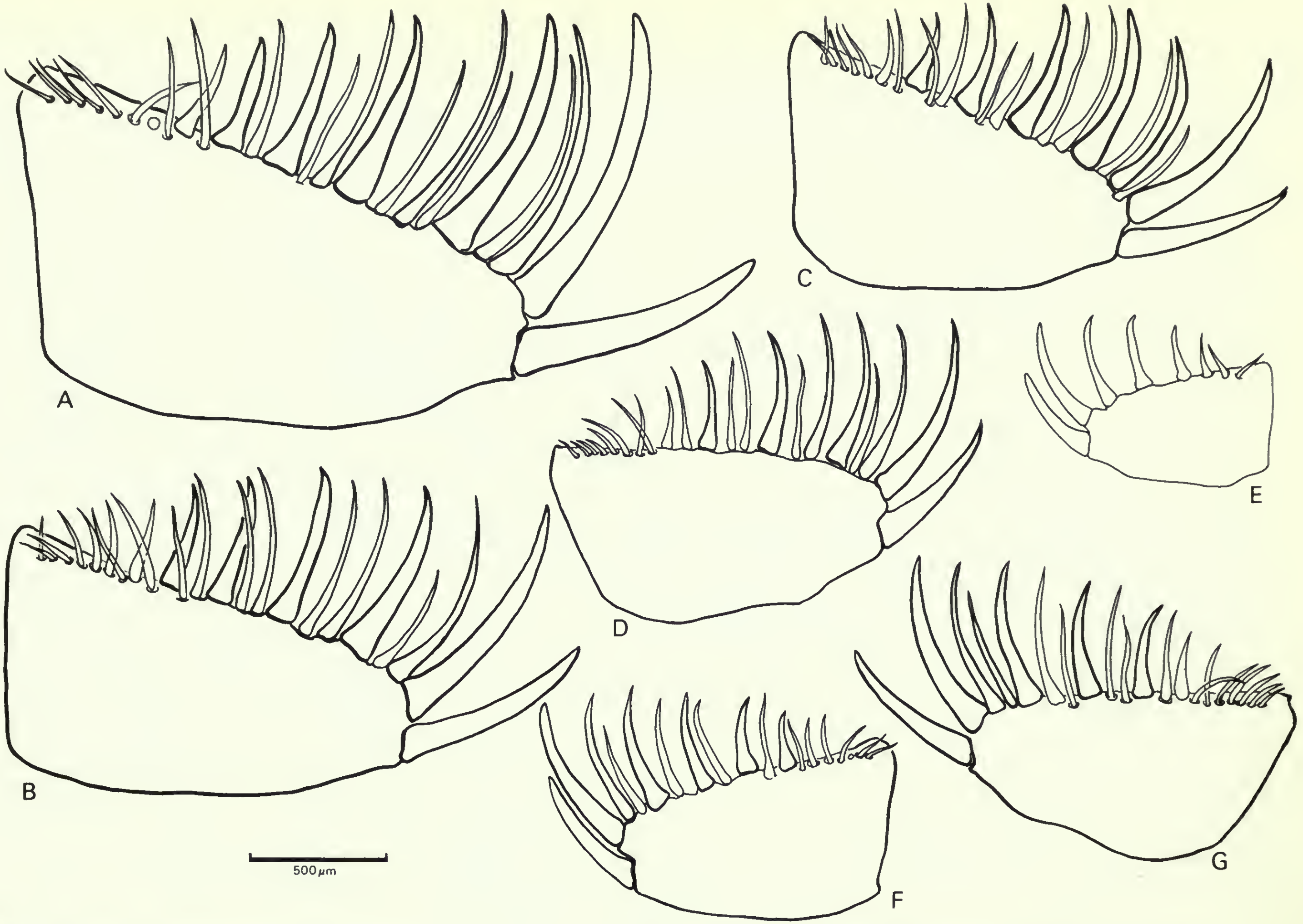

Fig. 11 *Azygocypridina imperialis* (Stebbing)
A-G: caudal furcae
A: female adult B.M.(N.H.) 1979.232
B: male adult B.M.(N.H.) 1979.239
C: male A-1 B.M.(N.H.) 1979.240.
D: female A-2 (holotype) B.M.(N.H.) 1911.11.8.3901
E: female A-3 B.M.(N.H.) 1979.235
F: male A-2 B.M.(N.H.) 1979.241
G: female A-2 (holotype) B.M.(N.H.) 1911.11.8.3901

The terminology used in the following descriptions is based on the comprehensive study of cypridinids by Skogsberg (1920) to which reference should be made for a discussion of structure, function and homology of the appendages. The letter notation of homologous setae, introduced by Skogsberg and adopted by Poulsen (1962) and Kornicker (1970, 1975), is used for the description of the first antennae, but not for other appendages, where the homologies between setae are less readily recognized.

First antenna. This appendage is seven-jointed and geniculate. The proximal ventral margin of the second podomere bears a cluster of seven setae; there are two short setae laterally, anterior to the previous group, and two other setae laterally and subterminally; there are about twenty setae on or near the dorsal margin. The third podomere carries seven setae ventrally and eighteen setae dorsally. The fourth podomere bears, distally, five ventral and five dorsal setae. Ventro-distally the fifth podomere has a long, annulate seta which bears many fine, filamentous setules. The sixth podomere has a single short, medial seta. The seventh podomere bears seven setae. The *a*-seta is short and finely pinnate; the *b*-seta is almost twice as long and bears, dorsally, numerous long, filamentous setules which in the male have spoon-like tips; the *c*-seta is about three times the length of the *b*-seta, bears identical, but fewer, setules, and is similarly dimorphic; the *d*-seta and *e*-seta are about the same length as the *b*-seta; the *f*-seta is about twice the length of the fifth podomere seta; the *g*-seta is slightly longer than the *f*-seta and bears numerous, long, filamentous setules.

Second antenna. The male endopodite is three-jointed, the first podomere bearing one long and three short setae proximally and six setae of different lengths medially. The second podomere carries a cluster of about ten setae medially. The third podomere is inflated and recurved with a long annulate seta arising proximally and with two short terminal setae. The female endopodite has a first podomere similar to that of the male. The second podomere bears a single annulate seta distally which is as long as the third podomere. The third podomere bears a long annulate seta terminally. The exopodite in both sexes is nine-jointed. The second to ninth podomeres each carry a long, strongly pinnate seta distally on the dorsal margin. In addition, the ninth podomere bears six other similar setae of varying lengths, the ventral one being much shorter than the others.

Mandible. The coxale endite is finely hirsute with two pectinate, terminal spines. The proximal ventral margin of the basale bears two stout, pectinate spines and about fourteen slender setae of varying lengths. Mid-ventrally there is a long, stout, pinnate seta. Distally, about 6–8 annulate setae of varying lengths form a curved row reaching the dorsal margin which bears three long, annulate setae, two distally and one medially. The exopodite carries two long, terminal setae ventrally, the proximal one being the longer. The first podomere of the endopodite bears six setae on the ventral margin, two being noticeably pinnate and another, shorter than the rest, terminating in a prominent aesthatasc. The second podomere carries a cluster of twenty to thirty setae dorsally and ten setae distally on the ventral margin. The endopodite terminates in two stout, chelate setae together with about four short setae.

Maxilla. The coxale bears a single, stout, hirsute seta. The exopodite bears two long, naked, terminal setae and a single shorter, annulate, pinnate seta on its outer margin, which is hirsute. The basale carries a single long, naked, annulate seta subterminally near to the base of the expodite and one long, naked, annulate seta near the base of the third endite. The medial margin bears about five to seven short setae. The endopodite carries about nineteen setae on two podomeres. Some are pectinate, some pinnate and others naked and annulate or filamentous. The first endite bears about sixteen long setae marginally, many with triaenid tips, and about four short medial setae. The second endite has numerous stout setae medially, about five fine setae terminally and two stout setae sub-terminally. There is a single long proximal seta. The third endite bears about thirteen varied setae marginally.

Fifth Limb. The epipodial vibratory plate carries about one hundred setae and the endites bear numerous, varied setae. The outer lobe of the third podomere of the expodite is hirsute and bears two hirsute, annulate setae terminally and one short, hirsute seta medially. The fourth podomere bears six naked, annulate setae on the distal lobe. The fifth podomere bears twelve hirsute, annulate setae on the distal lobe and eight naked, annulate setae on the proximal lobe.

Sixth Limb. The epipodial appendage consists of nine setae. The terminal podomere is divided, the distal lobe bearing eight pinnate setae, the proximal lobe bearing at least fifty-four setae of various types, some pinnate, others hirsute or naked. The first endite has six setae, the second has eight and the third has seventeen setae. The fourth endite bears ten setae terminally and two setae medially.

Seventh Limb. In the male, the seventh limb is vermiform and annulate, and bears about forty marginal setae distally. The terminal part consists of paired jawlike processes. One bears three stout 'teeth', the other a single hooked 'tooth'. The seventh limb of the female is similar but bears sixty marginal setae and the 'jaws' bear nine and six setae. In both sexes the distal portion of each marginal seta bears up to eight 'bells'.

Furcae. Between twenty-two and twenty-nine strong chelate spines are borne on each lamella. The first spine is always shorter than the second. The 'major' and 'minor' spines are irregularly arranged (see Table 3). The 'minor' spines are always more than half the length of the 'major' spines.

Brush-like appendage. This is elongate and bears about twelve terminal setae. Absent in the female.

Male copulatory appendage. Each of the paired appendages has a small squat penis. The outer lobe of each appendage bears numerous, stout setae and a distal hooked process bearing about four or five setae on each flank. The inner lobe bears numerous setae and has a globular, serrated lip.

Comparison of *A. imperialis* and *A. africanus*

Table 4 shows the mean dimensions of the carapace of adult and A-1 instars of *A. imperialis* and *A. africanus*. The numbers of specimens measured for this comparison are shown and the dimensions are expressed both as absolute values (in mm) and as a percentage of carapace length (in brackets). Adult and juvenile males and females of *A. imperialis* have very similar shapes. *A. africanus* (both female and A-1♂) is much larger and somewhat less inflated than *A. imperialis* but has a similar profile in lateral view.

A comparison of *A. imperialis* and *A. africanus* revealed several specifically diagnostic meristic characters of the antennae (see Fig. 2). The female *A. africanus* has, proportionately, much larger *c*-, *f*- and *g*-setae, and much shorter *d*-setae on the first antennae than either sex of *A. imperialis*. In addition, the terminal seta of the exopodite of the second antenna is comparatively much shorter in *A. africanus*. These differences are also seen when comparing the antennae of A-1 males of each species (see Fig. 3). Other small differences in relative length of antennal setae may eventually prove to be specifically diagnostic characters, but more specimens must be measured before this can be decided with certainty. Comparative measurements of at least twenty specimens of each species would be required.

Ontogeny and sexual dimorphism in *Azygocypridina*

The size distribution of one hundred and three specimens of *A. imperialis* from the N.E. Atlantic is shown in Figures 1a and 1b. No geographical grouping of specimens collected at different latitudes is apparent (Fig. 1a). Since some overlap in carapace size between instars was found, specimens were allocated to the sex and instar groups shown in Text-figure 1b on the basis of anatomical differences in the 2nd antenna.

All the adult specimens of *A. imperialis* examined, and all adults of previously described *A.* spp., bear seven setae terminally on the exopodite of the second antennae. A-1, A-2, A-3, A-4 and A-5 instars of *A. imperialis* were found to have 6, 5, 4, 3 and 2 setae, respectively, in this position.

The addition of a seta at each moult is probably a feature common to all species of *Azygocypridina*. An examination by the author of a male *A. africanus*, which on the basis of carapace size was consistent with being an A-1 instar, showed that there were six setae terminally. A single juvenile from within the carapace of a female *A. africanus*, examined by Stebbing (1901), had only a single terminal seta, which suggests that it was an A-6, or earlier, instar.

Dimorphism of the second antennae was used to determine the sex of adults and juveniles of *A. imperialis*. At all stages from A-5 to adult the third podomere of the endopodite of the 2nd antenna of both sexes bears a long seta. In females this seta arises terminally whereas in males it is non-terminal. This sexual dimorphism first appears in the A-3 instar, at which stage the seta in males is only just non-terminal. (See Fig. 10F.) In subsequent male instars the podomere becomes progressively stouter while the seta arises proportionately further from the distal end. In adult males, the third podomere is grossly enlarged and recurved, the seta arising basally (see Fig. 8A). All specimens of the A-4 and A-5 instars examined had terminal setae. While it is possible that all of these specimens were females, it is more likely that *A. imperialis* does not exhibit sexual dimorphism of the 2nd antennae until the A-3 instar since even at that stage, the sexual dimorphism is not pronounced.

Sexual dimorphism at the adult stage is not confined to the anatomy of the 2nd antenna. The *b*- and *c*-setae of the first antennae have spoon-like tips in the male, but pointed tips in the female; the seventh limb of the sexes differs most noticeably in the number of marginal setae, and in the structure of the terminal 'jaws' (see diagnosis for detailed description); paired copulatory appendages and brush-like organs are possessed by the male alone.

Carapace dimorphism is distinct at the adult stage, females being much larger than males. At the A-1 stage there is some overlap of the size ranges of the male and female groups (see Fig. 1b), but in general the females tend to be larger than the males. No A-2 females were found. At the A-3, A-4 and A-5 stages no sexual dimorphism of the carapace was observed.

Brooks (1886), working on Stomatopoda, postulated that the relationship between the carapace lengths of successive instars was a geometric progression with a ratio (growth factor) of approximately 1·25. Fowler (1909), who was the first to apply this concept to the Ostracoda, found that the growth factors of some halocyprid species ranged from 1·26 to 1·78. Przibram (1931) suggested that an increase in linear dimensions at each moult by a factor of 1·26 (i.e.$\sqrt[3]{2}$) results from the doubling of carapace volume after ecdysis. This relationship exists only when the shape of the carapace remains constant from one instar to the next. Anderson (1964) has suggested that the figure of 1·26 may be a statistical artifact. Using an alternative logarithmic method, he has shown that there is a wide variation around 1·26 in the growth factors of different ostracod species.

The carapace of *A. imperialis* retains the same subspherical shape in successive instars, a fact that can be demonstrated by a simple comparison of length : height : breadth ratios for a series of instars. From the results recorded in Table 5 it appears that there is considerable variation in the growth factors of instars of *A. imperialis*, indicating that the volume enclosed by the carapace is not exactly doubled at each moult. However, the average growth factor for the species is 1·27, the value for females being 1·29 and for males, 1·23. The mean growth factor for the maturation moult is much higher for females than for males. Presumably, this additional increase in volume by females provides space for the storage of ova within the carapace.

The holotype of *A. imperialis* bears 5 terminal setae on the exopodite of its second antenna. This number of setae is indicative of an A-2 instar. The length of the carapace, given by Brady and Norman (1896) as 7·00 mm is greatly in excess of the length expected for an A-2♀ instar of *A. imperialis*. Brady and Norman's measurements may have been inaccurate due to the distortion of the specimen in the net. Alternatively, this specimen may

Table 5 Mean and range of carapace lengths and mean growth factors of 103 specimens of *Azygocypridina imperialis*.

	Adult ♀	Adult ♂	A-1 ♀	A-1 ♂	A-2 ♀	A-2 ♂	A-3 ♀	A-3 ♂	A-4	A-5
Mean Length (mm)	9·48	7·45	6·98	6·36	—	4·87	4·22	4·39	3·12	2·66
Length Range (mm)	8·33–10·13	6·84–8·16	6·50–7·65	6·16–6·65	—	4·70–5·00	4·22	4·30–4·50	2·90–3·52	2·50–2·72
Mean Growth Factor	1·36	1·17	—	1·31	—	1·11	1·35	1·4	1·17	—
Number of Specimens	21	44	9	10	—	3	1	3	8	4

be an exceptionally large A-2♀. Unfortunately, only fragments of the carapace of Brady and Norman's specimen remain and it is, therefore, impossible to verify their recorded measurements.

Fecundity of *Azygocypridina*

In common with other cypridinids, females of *Azygocypridina* spp. retain clusters of ova within the carapace until hatching occurs. Four specimens of *A. imperialis* examined were ovigerous females. One was left unopened but the other three were found to contain respectively 31, 42 and 65 ova, all about 0·45 mm in diameter, within the posterior part of the carapace. Ova of similar size were observed by the present author within the carapace of an unopened specimen of *A. africanus*.

Stebbing (1901) reported finding some early instars inside a specimen of *A. africanus*, but he did not observe any ova. Kornicker (1969) and McKenzie (1968) both reported the presence of ova within the carapaces of their species of *Azygocypridina*, but they did not indicate the size of the clutches. However, McKenzie stated that the ova were numerous and about 0·15 mm in diameter. Examination of the lectotype of *A. africanus*, designated herein, revealed about 120 sub-spherical cells, about 0·15 mm in diameter, adhering to the marginal setae of the seventh limb and to other appendages. Similar cells are not uncommon in midwater halocyprids and are thought to be epibionts (Angel, pers. comm.). Thus, McKenzie's 'ova' may have been similar epibionts, or, his observation may indicate that his shallow-living *A.* sp. has a reproductive strategy different from that of deeper water forms.

The function of the vermiform seventh limb

The function of the vermiform seventh limb, found in all cypridinids, has been the subject of much debate. As early as 1840, Milne-Edwards described the seventh limbs as 'pattes ovifères' (oviferous feet) and ascribed to them an egg-bearing function. This opinion was shared by Baird (1848, 1850), and Claus (1865). Zenker (1854), however, suggested a cleaning function for these appendages. This view was also held by F. Müller (1870) and G. W. Müller (1894). The latter author observed the appendages 'moving over the back, between the gills and particularly between the eggs', and Stebbing (1899) stated that the vermiform limb of *Asterope* is used to clean the inside and outside of the valves, other limbs and the eggs. Skogsberg (1920) reported that the seventh limbs appeared late in ontogeny and were therefore less likely to be exclusively for cleaning than for some aspect of reproduction in maturity. The seventh limb shows only very little sexual dimorphism and its use in egg care is brought into question since the males are not known to play any part in brood care. However, in *Sarsiella* alone, the male lacks a seventh limb, suggesting that at least in this genus its function, whatever it may be, is essential only to the female.

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Descriptions of two new and one poorly known species of the genus *Caligus* Müller, 1785 (Copepoda: Siphonostomatoida)

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Introduction

Caligus dubius was first described by Scott in 1894 from material collected from the plankton of Loanda Harbour, Gulf of Guinea. Both sexes were present in Scott's material but his inadequate description was based only on the female. The single subsequent record of *C. dubius* is that of Leigh-Sharpe (1934) who assigned some material from the Siboga expedition to *C. dubius*. No host or station data are available for Leigh-Sharpe's material. The type material of *C. dubius* is stored in the collections of the British Museum (Natural History) and reexamination of this material has revealed several significant differences from the specimens described by Leigh-Sharpe (1934). The female of *C. dubius* is redescribed and the male is described for the first time. Leigh-Sharpe's material is redescribed as a new species, *C. sibogae*, belonging to a well defined group of species within the genus *Caligus*. The diagnostic features of this group, called here the *macarovi*-group, are described and its 28 member species are listed. A second new species, *C. antennatus*, is described from material sent from Kuwait by Dr I. U. Tareen. This species is also referred to the *macarovi*-group.

Specimens were dissected and examined in lactophenol using phase contrast microscopy. Some specimens of *C. antennatus sp. nov.* were freeze dried and examined by scanning electron microscopy. Drawings were made either using a camera lucida or by tracing from micrographs.

Caligus dubius Scott, 1894

Caligus dubius T. Scott, 1894 : 130, pl. XIV, fig. 22.
nec. Caligus dubius : Leigh-Sharpe, 1934 : 19–21, figs 17, 18.

ADULT FEMALE. Dorsal shield (Fig. 1A) subcircular with marked posterior sinuses, and comprising half the total body length. Free margin of thoracic portion of dorsal shield extending beyond posterior tips of lateral portions. Genital complex distorted in preserved syntype but approximately 1·5 times longer than broad, greatest width near posterior margin and tapering slightly anteriorly (according to Scott, 1894 : pl. XIV, fig. 22). Abdomen 1-segmented, 3 times longer than broad. Caudal rami about 2·5 times longer than broad and armed with 3 long plumose setae and 3 short setae. Body length of syntype female 3·6 mm. Egg strings about 1 mm in length and containing 8 eggs.

First antenna of usual structure for genus but with many armature elements missing from syntype. Second antenna (Fig. 1F) with a posteriorly directed spinous process on basal segment, middle unarmed, terminal segment subdivided into a basal portion carrying 2 small setae and a claw-like apical portion. Post antennal process (Fig. 1D) with a small base bearing 2 multiple setules and a long slender tine. Mandible of usual form for genus. First maxilla (Fig. 1E) anterior process with 3 naked unequal setae, posterior process with a simple slender tine. Second maxilla (Fig. 2A) with long flabellum on brachium (see Kabata,

Bull. Br. Mus. nat. Hist. (Zool.) **39** (3) : 161–178   Issued 27 November 1980

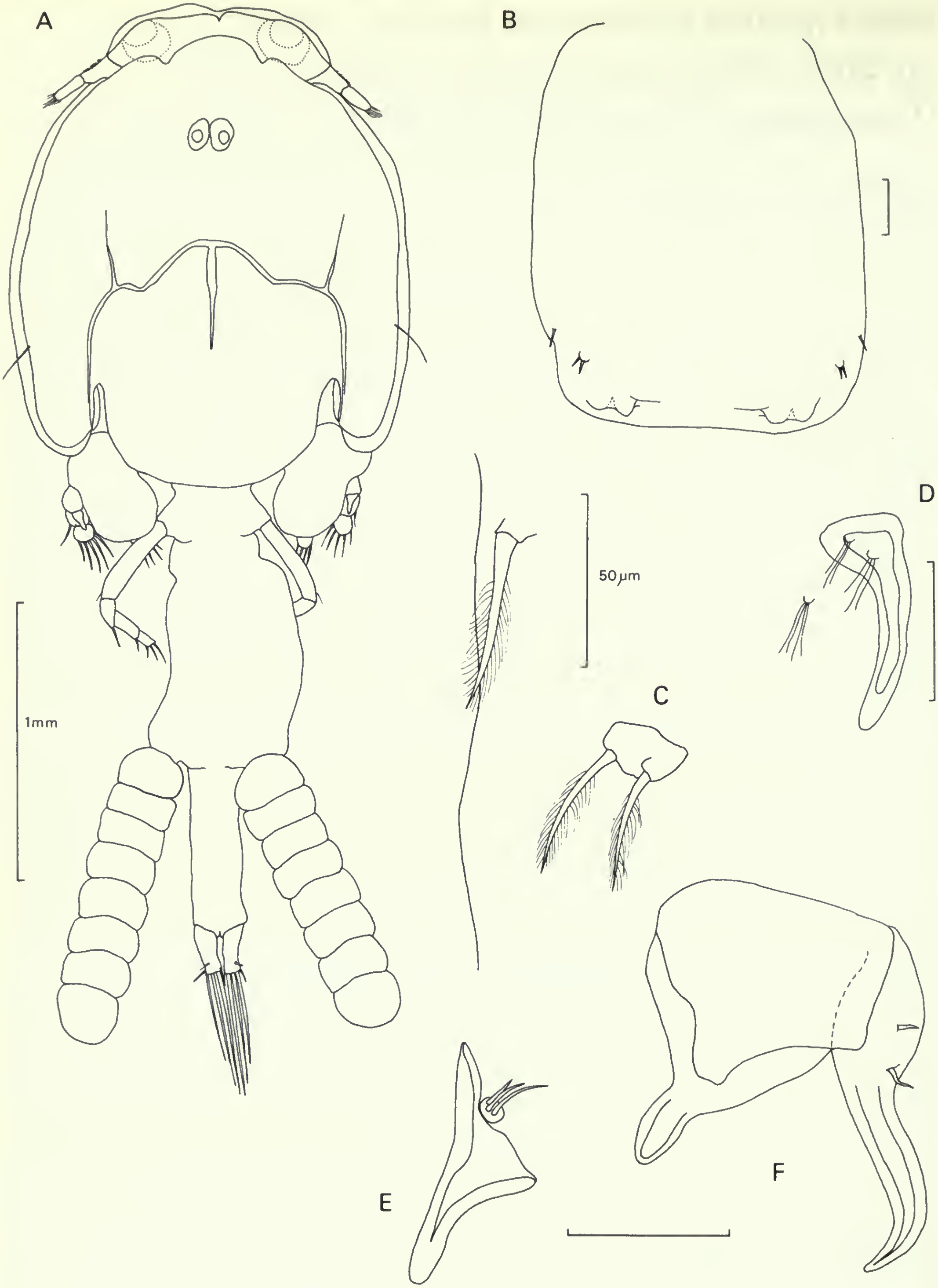

Fig. 1 *Caligus dubius* syntype ♀. A, dorsal; B, genital complex, ventral; C, leg 5, ventral; D, post antennal process, ventral; E, first maxilla, ventral; F, second antenna, ventral. Scales 100 μm unless otherwise stated.

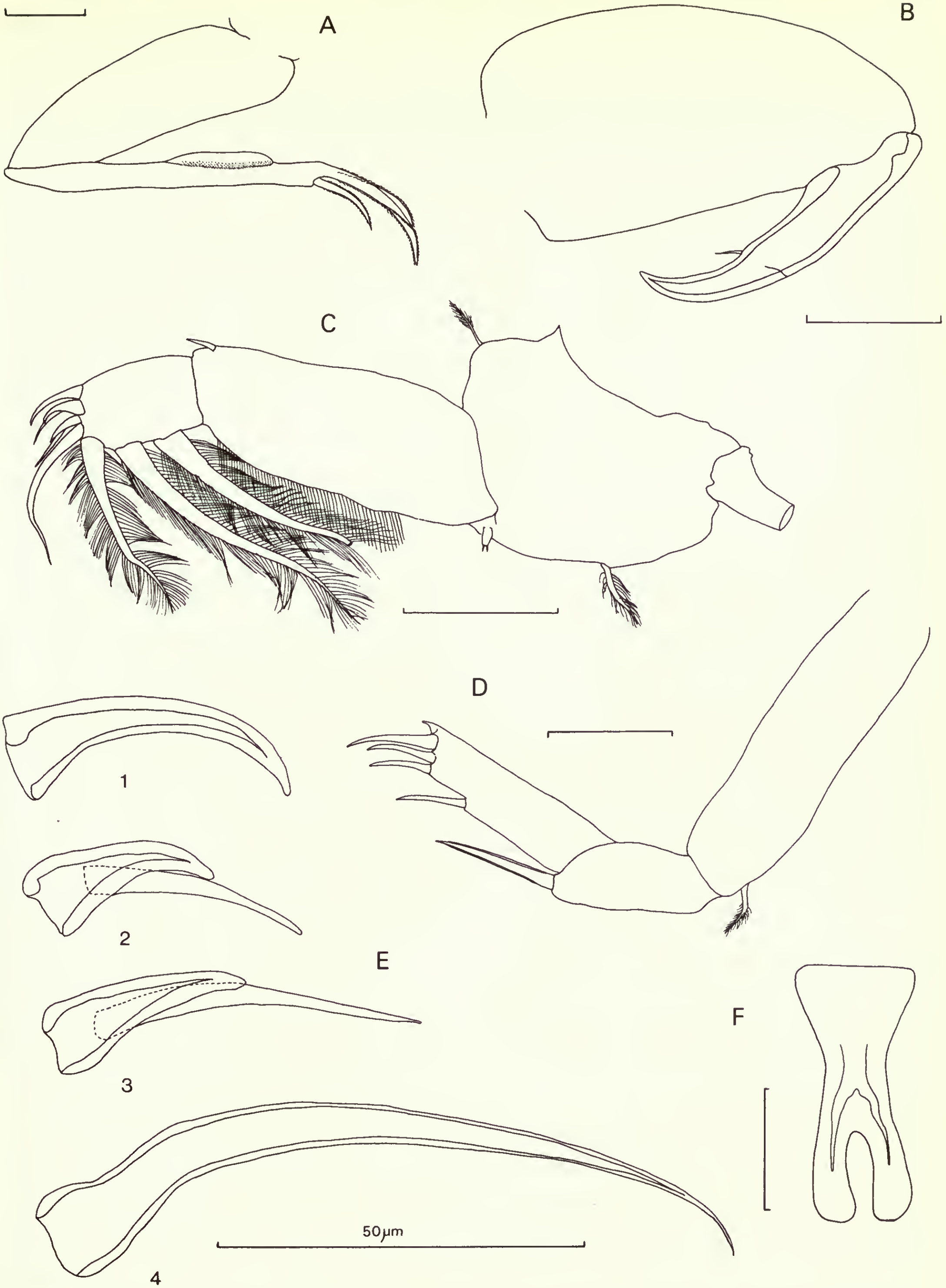

Fig. 2 *Caligus dubius* syntype ♀. A, second maxilla, ventral; B, maxilliped, posterior; C, leg 1, ventral; D, leg 4, ventral; E, spines 1 to 3 and seta 4 from distal margin of leg 1 exopod; F, sternal furca, ventral. Scales 100 μm unless otherwise stated.

1979 for new morphological terms); calamus nearly twice as long as canna and bearing 4 strips of serrated marginal membrane running obliquely along its length; canna with bilateral serrated membranes. Maxilliped (Fig. 2B) with robust basal segment and curved terminal claw bearing a single seta on concave margin. Sternal furca (Fig. 2F) small, with parallel spatulate tines.

Leg 1 (Fig. 2C) vestigial endopod with 2 minute spinules on apex; exopod segment 2 with 3 long plumose setae on posterior margin and 4 distal margin elements; spine 1 (Fig. 2E—1) simple, spines 2 & 3 (Fig. 2E—2, 3) each bearing a slender accessory process that extends beyond the tip of the spine itself, seta 4 (Fig. 2E—4) long and naked. Leg 2 (Fig. 3A) sympod segment 1 with a plumose seta on posterior margin and a swelling bearing a slender setule on ventral surface; endopod segment 2 with a single row of pinnules along lateral margin; exopod segment 1 with a well developed, obliquely-directed spine at outer distal angle, segment 2 with a small spine at outer distal angle, segment 3 with 1 minute and 1 small spine on outer margin, an apical seta and 5 plumose setae on inner margin. Leg 3 a broad flattened plate as in other species of the genus; endopod (Fig. 3C) 2-segmented, lateral margins of both segments provided with rows of long pinnules; segment 1 with 1 inner plumose seta, segment 2 with 6 distal and inner margin plumose setae; exopod (Fig. 3B) 3-segmented, segment 1 with a broad spatulate spine subapically on distal margin and a single setule on lateral margin, segment 2 longer than broad, with an inner margin plumose seta and with a row of pinnules and a long setiform spine distally on outer margin, segment 3 with a row of pinnules and 3 slender spines on outer margin and 4 unequal plumose setae on distal margin. Leg 4 (Fig. 2D) 3-segmented; second segment with a long apical spine armed with bilateral membranes; third segment (Fig. 3D) with 1 lateral and 3 apical spines each with a pecten situated at its base; lateral and outermost spines both provided with a single strip of smooth membrane along lateral margin, inner and middle apical spines unarmed. Leg 5 (Fig. 1B, C) situated postero-laterally on ventral surface of genital complex, comprising an inner process bearing 2 apical plumose setae and a small outer process bearing a similar seta. Leg 6 represented by a plate near oviduct opening, apparently unarmed.

ADULT MALE. Dorsal shield (Fig. 4A) slightly more oval in outline than female, and comprising just over half of total body length. Genital complex (Fig. 4C) about 1·7 times longer than maximum width (at mid-point). Abdomen 2-segmented, about 3 times longer than width at base; second segment about 20% longer than first. Caudal rami as in female. All appendages as in female except second antenna, maxilliped and legs 5 and 6. Second antenna (Fig. 4B) 3-segmented; basal segment with a corrugated adhesion pad; middle segment with subrectangular adhesion pad proximally and a small adhesion pad on distal swelling; terminal segment cup-shaped fitting around distal swelling on middle segment, armed with 2 setae on inner concave surface. Maxilliped (Fig. 4D) with robust basal segment bearing a large myxal process, concave apically to receive tip of terminal claw; curved terminal claw heavily chitinized and with a robust spine near apex on concave margin. Leg 5 (Fig. 4C) difficult to observe due to poor state of preservation, but with inner process bearing 2 setae as in female. Leg 6 possibly represented by a broad plate, but partially obscured by particles adhering to specimen. Body length of males ranging from 2·6 to 4·4 mm, with a mean of 3·6 mm (based on 5 syntype specimens).

MATERIAL EXAMINED. 1 ♀, 5 ♂♂ syntypes of *Caligus dubius* : surface tow net hauls in Loanda harbour and Appi, Gulf of Guinea (Scott, 1894). B.M.(N.H.) 1893.4.22.94–97.

REMARKS. Several species of *Caligus* possess the combination of an abdomen in the female that is about 3 times longer than wide and a 3-segmented leg 4 bearing 1 lateral and 3 apical spines on the terminal segment. The majority of these species, however, belong to a group of species (the *productus*-group) characterized by the absence or marked reduction of the 3 plumose setae on the posterior margin of leg 1 exopod segment 2, and often by the presence of large denticles or spinules on the lateral margin of leg 2 endopod segment 2. *C. dubius* does not exhibit these characters. *C. dubius* appears to be more closely related to *C.*

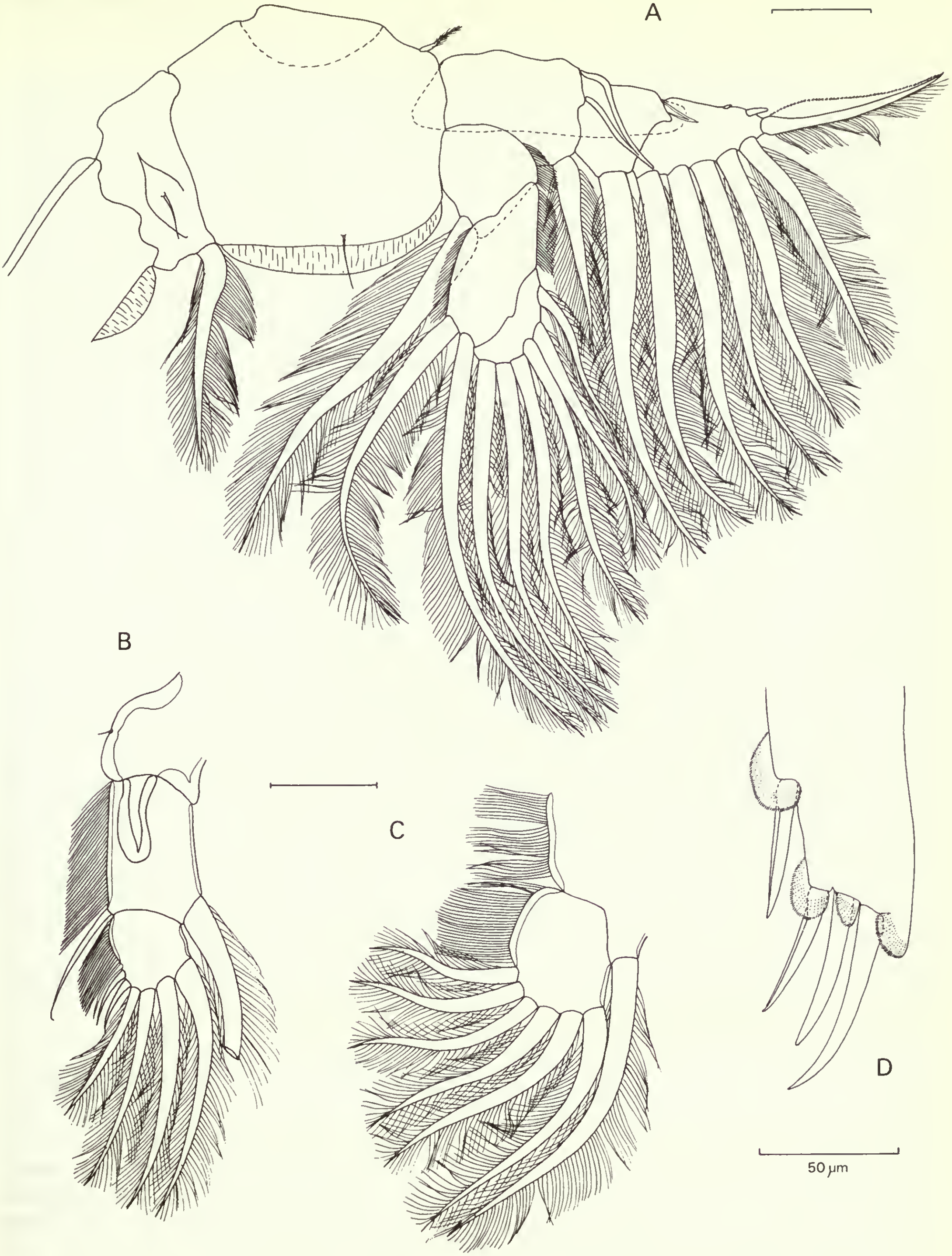

Fig. 3 *Caligus dubius* syntype ♀. A, leg 2, ventral; B, leg 3 exopod, ventral; C, leg 3 endopod, ventral; D, distal tip of leg 4, ventral. Scales 100 µm unless otherwise stated.

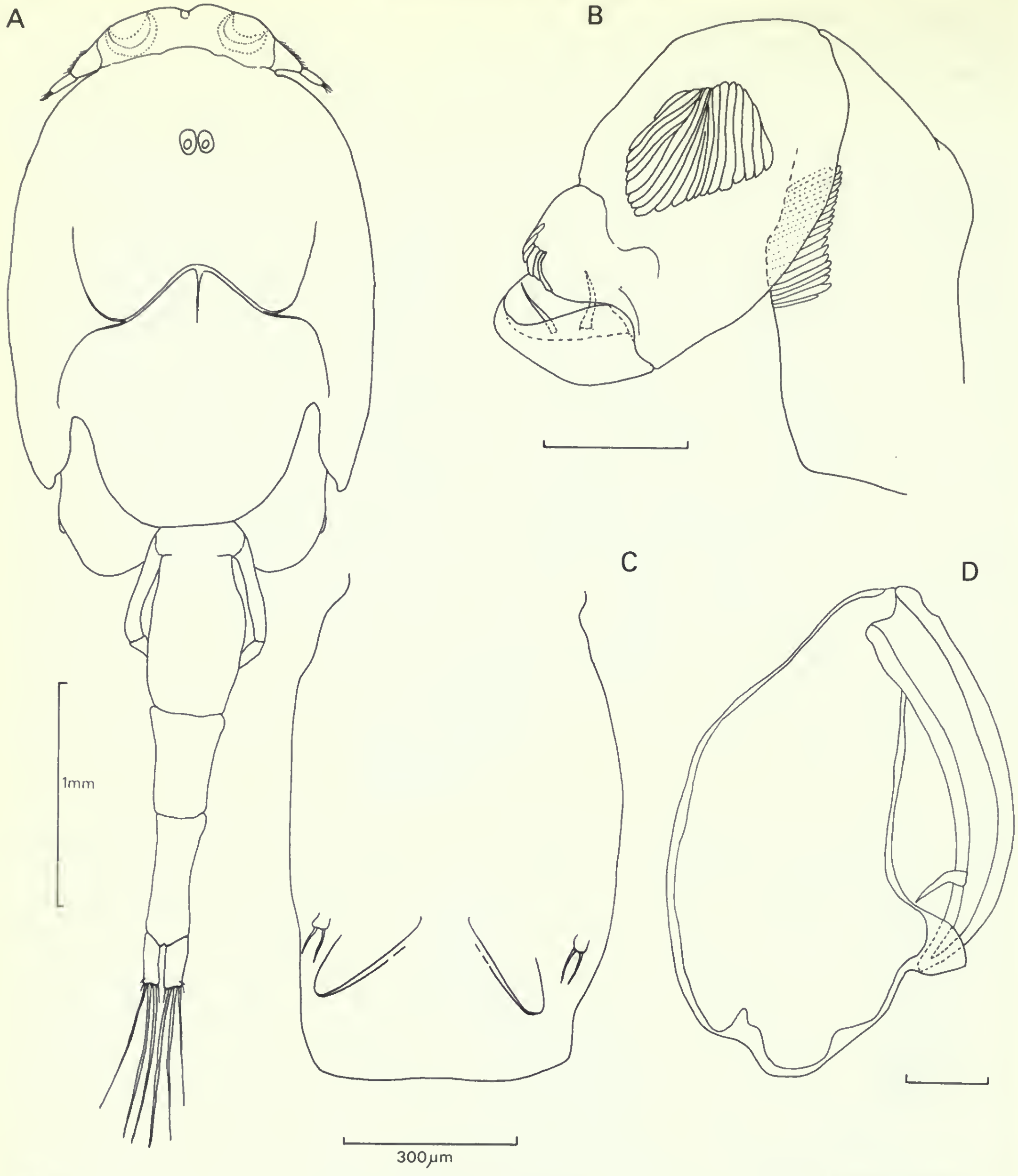

Fig. 4 *Caligus dubius* syntype ♂. A, dorsal; B, second antenna, ventral; C, genital complex, ventral; D, maxilliped, posterior. Scales 100 µm unless otherwise stated.

elongatus Nordmann, 1832 which it resembles in the configuration of the terminal spines of leg 1 and in the structure of the second antenna, but it can be readily separated from the species close to *C. elongatus* by the possession of an elongate abdomen and by the presence of a myxal process on the male maxilliped.

C. dubius differs from the specimens referred by Leigh-Sharpe (1934) to *C. dubius* in the shape of the genital complex and of the abdomen, in the absence of a lateral spine from the terminal segment of the leg 4, in the position of the myxal process on the male maxilliped and in other details of the appendages.

Caligus sibogae sp. nov.

Caligus dubius: Leigh-Sharpe, 1934 : 19–21, figs 17, 18.

ADULT FEMALE. Dorsal shield (Fig. 5A) subcircular, with marked posterior sinuses, and comprising just over half the total body length; shield split on left side in holotype. Free margin of thoracic portion of dorsal shield extending beyond posterior portions of lateral portions. Genital complex subrectangular, about 1·3 times longer than wide, with nearly parallel lateral margins and small postero-lateral processes. Abdomen approximately 1·8 times longer than broad, almost as wide as genital complex at level of greatest width. Caudal rami longer than wide and with armature elements missing from holotype. Body length of holotype female 5·6 mm.

First antenna of usual form for genus. Second antenna (Fig. 5B) with slender posteriorly directed process on basal segment and strongly curved claw-like terminal segment bearing 2 small setae. Post antennal process (Fig. 5C) comprising a small basal area with 2 simple setules and a slender tine. Mandible of usual structure for genus. First maxilla (Fig. 5D) consisting of an anterior process bearing 3 naked setae and a simple posterior tine. Second maxilla (Fig. 5E) with spiniform flabellum on brachium and with small irregular serrations along its posterior margin; calamus nearly twice as long as canna, both armed with strips of serrated membrane. Maxilliped typical of genus, without processes in myxal area. Sternal furca (Fig. 5F) with spatulate tines.

Leg 1 (Fig. 6A) exopod segment 2 with 3 long setae on posterior margin; each of these setae with a plumose medial margin and bearing long pinnules on proximal quarter of outer margin and a row of close set, fine short pinnules resembling a striated membrane in appearance along remainder of outer margin. Distal margin with 4 elements (Fig. 6B); spines 1, 2 and 3 similar, each with an accessory process at about 1/3 of its length; seta 4 long, simple and with small denticulations distally: seta 4 situated ventral to spine 3 on distal surface of segment. Leg 2 (Fig. 6C) endopod segment 1 with a row of pinnules at its outer distal angle; segment 2 with an outer row of pinnules; exopod segments 1 and 2 with large spines at outer distal angles, each spine directed obliquely over ventral surface of ramus and armed with a strip of smooth membrane on outer margin and a few small denticulations on inner margin; segment 3 with 1 unarmed spine and 1 spine armed with smooth membrane unilaterally on outer margin, 1 apical seta and 5 plumose setae on inner margin. Leg 3 of usual structure for genus. Exopod segment 1 with spine on distal margin missing from holotype, other armature elements as in male (Fig. 6D). Leg 4 (Fig. 6E) 3-segmented; second segment with long unarmed apical spine, third segment with 3 distal spines only, each with a long pecten at its base (Fig. 6F) and with a single strip of smooth membrane along its concave margin. Leg 5 (Fig. 5G) situated postero-laterally on ventral surface of genital complex, comprising an inner process bearing 2 plumose setae and an outer process from which the armature element is missing in the holotype but which bears a single seta according to Leigh-Sharpe (1934).

ADULT MALE. Dorsal shield (Fig. 7A) as in female but with wider posterior sinuses. Genital complex (Fig. 7B) about as long as wide, with greatest width in posterior third. Abdomen 2-segmented, about 1·7 times longer than wide; second segment about twice as long as first. Caudal rami as in female. All appendages as in female except second antenna, post antennal process, maxilliped and legs 5 and 6. Second antenna (Fig. 7C) 3-segmented; basal segment elongate and bearing a small adhesion pad on ventral surface; middle segment elongate and bearing 1 adhesion pad on dorsal surface and 2 distally on ventral surface; terminal segment small, with broad basal portion armed with 2 setae and a trilobed claw. Post antennal process (Fig. 7D) as in female but with relatively longer tine. Maxilliped (Fig. 7E) with robust basal portion bearing a large myxal process; curved terminal claw heavily chitinized, with an incomplete suture line near the tip (Fig. 7F) and a small spine on concave margin near apex. Leg 5 (Fig. 7B) probably incomplete but with an inner process bearing 2 small setae. Leg 6 represented by a broad flattened process carrying 2 small setae apically.

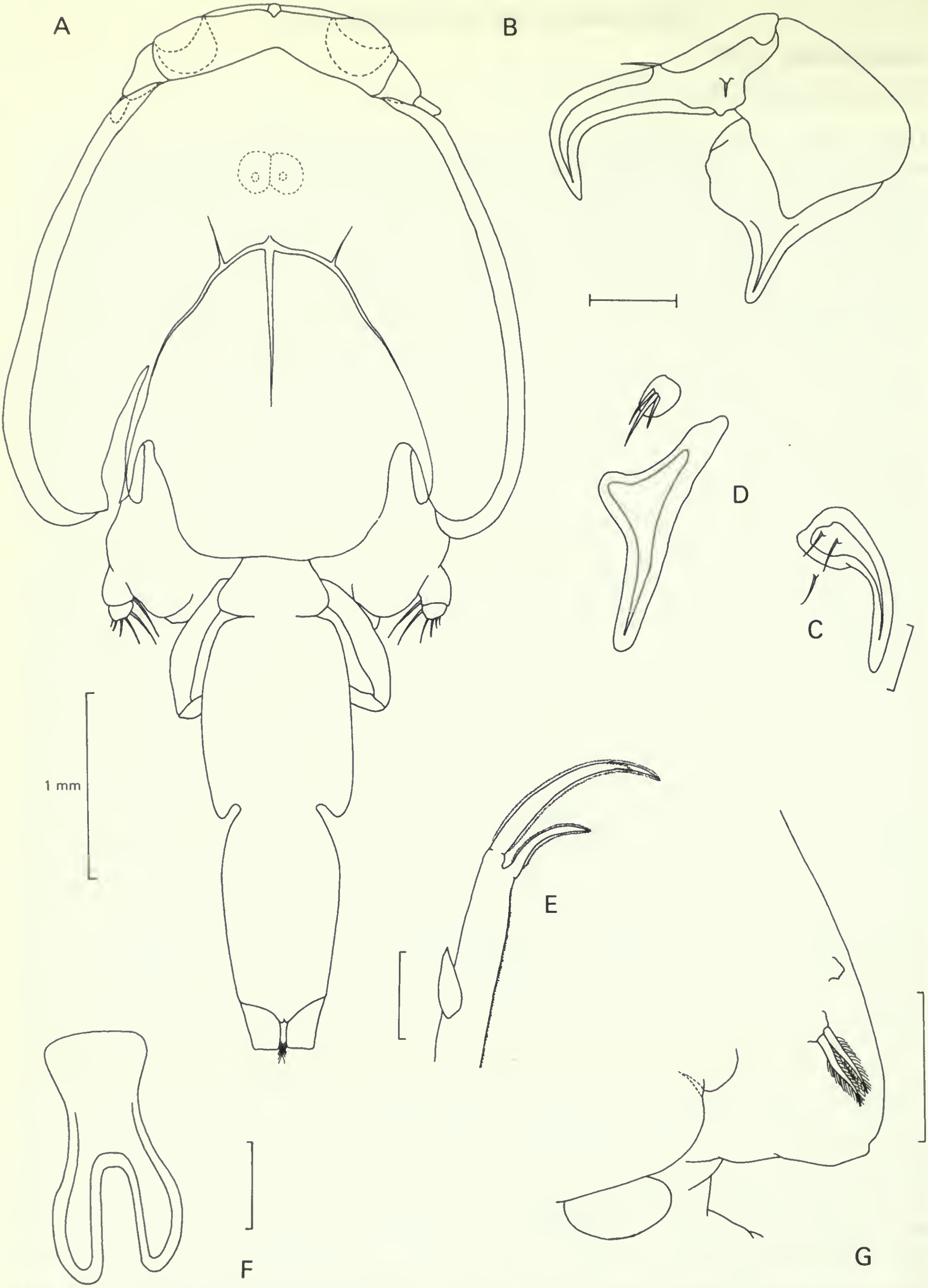

Fig. 5 *Caligus sibogae* sp. nov. holotype ♀. A, dorsal; B, second antenna, ventral; C, post antennal process, ventral: D, first maxilla, ventral; E, tip of second maxilla, ventral; F, sternal furca, ventral; G, postero-lateral angle of genital complex, ventral. Scales 100 µm unless otherwise stated.

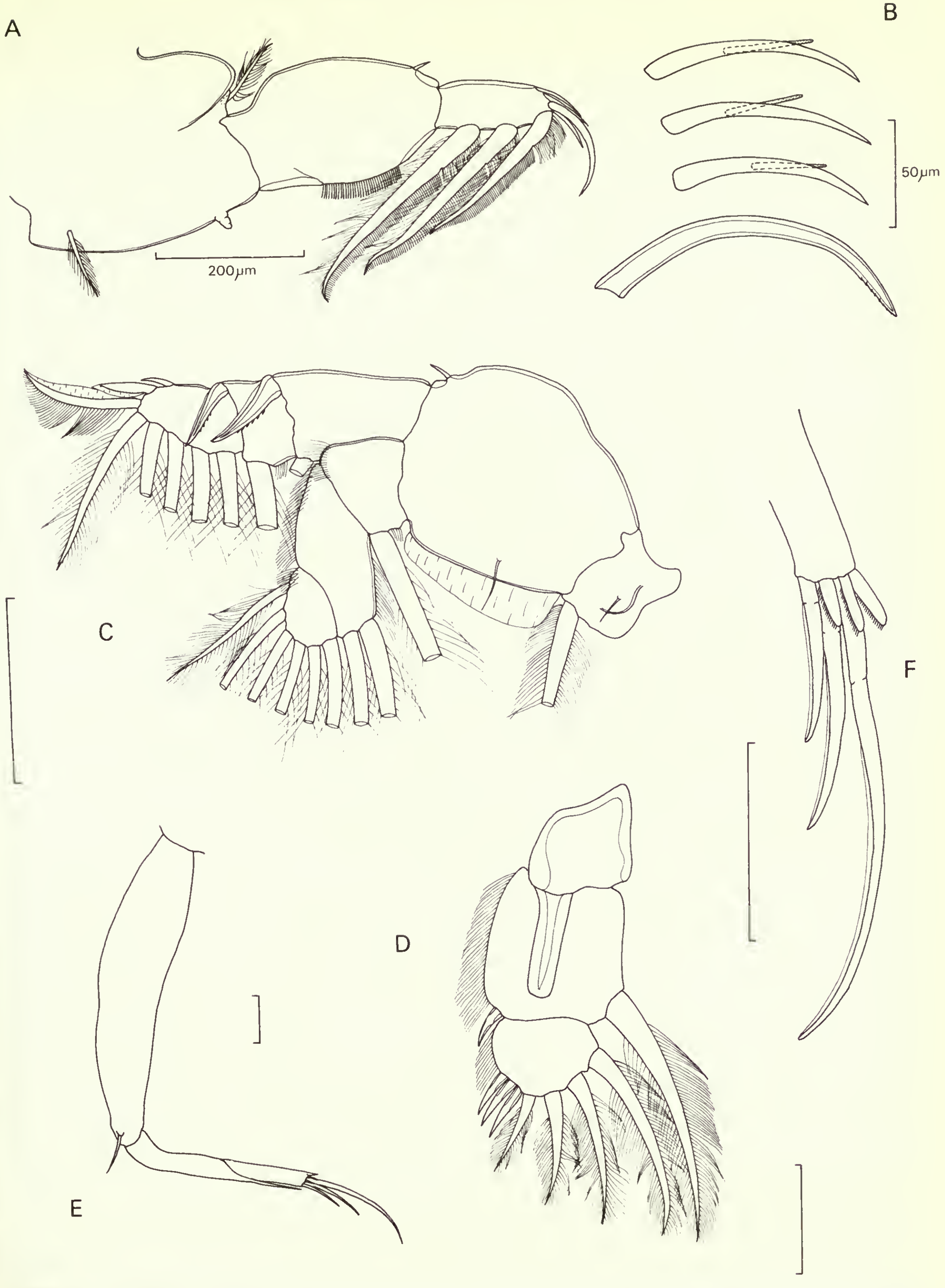

Fig. 6 *Caligus sibogae* sp. nov. A, holotype ♀ leg 1, ventral; B, spines 1 to 3 and seta 4 from distal margin of leg 1 exopod; C, leg 2, ventral; D, paratype ♂ leg 3 exopod, ventral; E, holotype ♀ leg 4, ventral; F, tip of leg 4, ventral. Scales 100 µm unless otherwise stated.

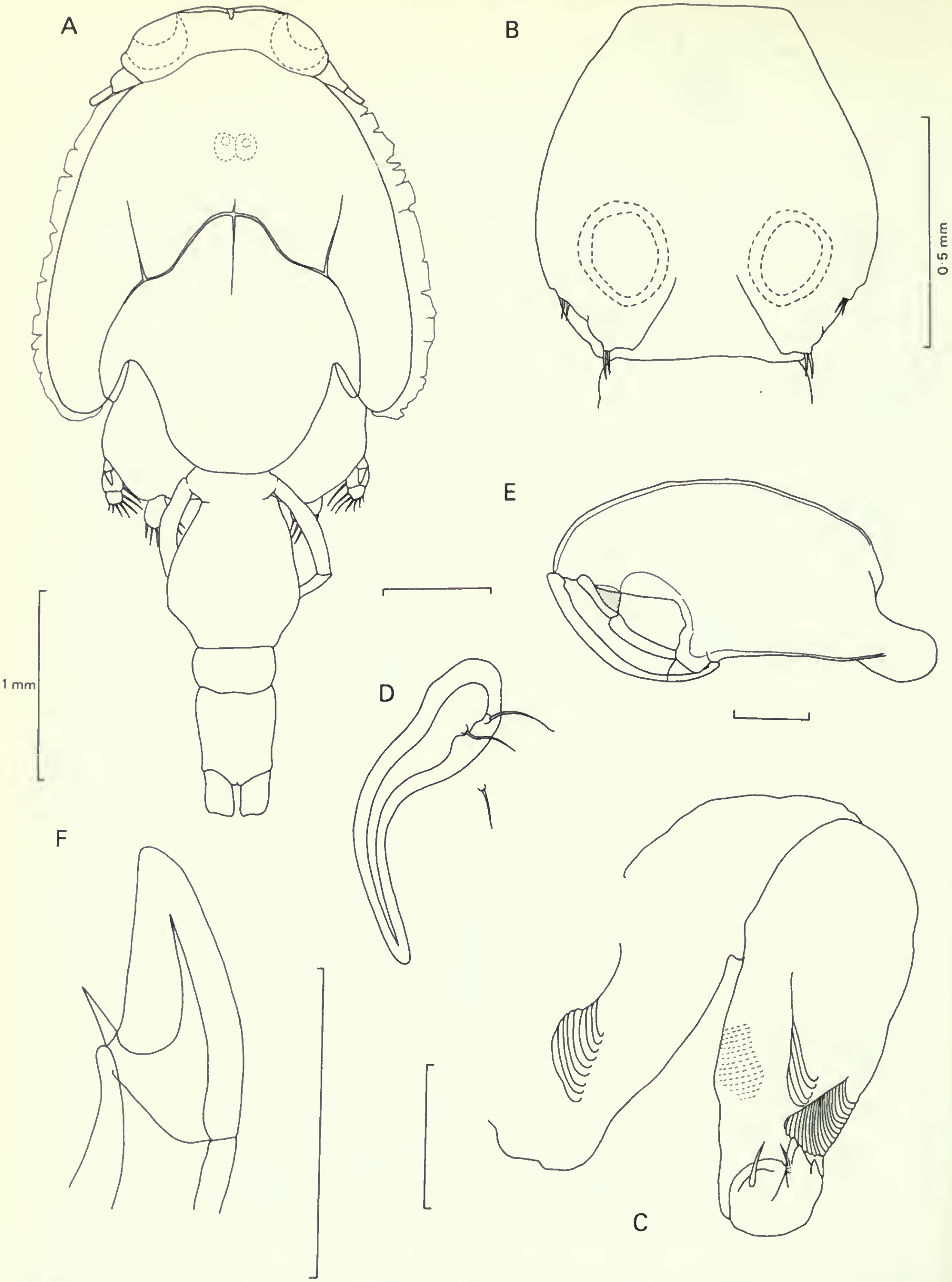

Fig. 7 *Caligus sibogae* sp. nov. paratype ♂. A, dorsal; B, genital complex, ventral; C, second antenna, ventral; D, post antennal process, ventral; E, maxilliped, posterior; F, tip of maxilliped claw, posterior. Scales 100 μm unless otherwise stated.

Body length of paratype males ranging from 4·0 to 4·2 mm, with a mean of 4·1 mm (based on 4 specimens).

MATERIAL EXAMINED. Holotype ♀, 4 ♂♂ paratypes: from Siboga expedition, identified as *Caligus dubius* by Leigh-Sharpe (1934). No host or locality data. Zoölogisch Museum Amsterdam Registration numbers Co.102.652 (Holotype ♀) and Co.102.653 (♂♂). The other female in the Siboga collection is referable to *C. savala* Gnanamuthu, 1948.

REMARKS. The new species, *C. sibogae*, belongs to a group of closely related species which we call here the *macarovi*-group. It contains the 28 species listed in Table 1. The *macarovi*-group is characterized by the presence in its members of the following combination of characters: 3-segmented leg 4 bearing 3 distal spines but no lateral spine on the terminal segment; leg 1 exopod segment 2 with 3 plumose setae (armed as in Fig. 6A) on posterior border and with 4 distal margin elements typically of the following configuration: spine 1 unarmed, spines 2 and 3 with an accessory process each, and seta 4 about twice as long as others, unarmed and positioned ventral to spine 3; 1-segmented abdomen in female and 2-segmented abdomen in male. In addition many memers of the group possess serrations or denticles along the posterior border of the brachium of the second maxilla, and a maxilliped with a distinct suture line and associated spine on the claw positioned near to its tip. The males typically possess a myxal process on the maxilliped whereas the females usually do not (although one is present in female *C. hamruri* Pillai, 1964). *C. hemiconiati* Capart, 1941, *C. lalandei* Barnard, 1948, *C. lolligunculae* Capart, 1941, *C. mordax* Leigh-Sharpe, 1934, *C. patulus* Wilson, 1937 and *C. tetrodontis* Barnard, 1948 may also belong to this group but are too poorly described to be placed there with certainty. Excluded from this group are *C. curtus* Müller, 1785, *C. brevicaudatus* Scott, 1901, *C. dasyaticus* Rangnekar, 1957, *C. epidemicus* Hewitt, 1971, *C. furcisetifer* Redkar, Rangnekar & Murti, 1949, *C. lepeophtheiropsis* Pillai, 1967, *C. microdontus* Heegaard, 1964, *C. minimus* Otto, 1821 and *C. tylosuri* (Rangnekar, 1956) all of which possess a 3-segmented leg 4 with only 3 distal spines on the terminal segment but differ in the configuration of the leg 1 armature elements. *C. balistae* Steenstrup & Lütken, 1861 and *C. raniceps* Heegaard, 1943 are also excluded as they possess a 1-segmented abdomen in the adult male. *C. cordiventris* Shiino, 1954 resembles members of this group in the leg 1 and leg 4 but differs in many other characters, including the possession of a 1-segmented abdomen in the male, a markedly bifid claw on the male second antenna and spinous processes on the leg 5 in both sexes.

C. sibogae can be distinguished from most of the species in the *macarovi*-group on the basis of body proportions, particularly the length to width ratio of the abdomen. Only *C. macarovi, C. longiabdominis, C. tenuicaudatus* and *C. thyrsitae* have an abdomen that is about 2 times longer than wide and equal to or only just shorter than the genital complex. It can be readily separated from *C. tenuicaudatus* which has caudal rami about 4·5 times longer than wide. It can be distinguished from *C. longiabdominis* by the absence of a posteriorly-directed process from the basal segment of the female second antenna, and by the much greater width of the genital complex relative to the abdomen in *C. longiabdominis*. It also differs from *C. macarovi* in this latter character and, in addition, in the presence of a patch of denticles on the sympod of the leg 1 in *C. macarovi*. The new species differs in body proportions from *C. thyrsitae* which has a much wider genital complex relative to the width of the abdomen. There are other differences between these two species in details of appendage structure and armature. The tines of the post antennal process and first maxilla are much longer in *C. sibogae* and the leg 4 of this species is much more slender and has relatively longer armature elements than in *C. thyrsitae*.

Caligus antennatus sp. nov.

ADULT FEMALE. Dorsal shield (Fig. 8A) subcircular with broad posterior sinuses and comprising 56% of total body length. Free margin of thoracic portion of dorsal shield extending beyond posterior tips of lateral portions. Genital complex slightly wider than long,

Table 1 Members of the *macarovi*-group within the genus *Caligus*
(References to the original and subsequent descriptions of these species can be found in Margolis, *et al.*, 1975)

Species	♀GCL : GCW	♀ABL : ABW	♀GCL : ABL	♀DSL : ABL	♂DSL : ABL	♂ABL1 : ABL2	Remarks
C. aduncus Shen & Li, 1959	0·9 : 1	0·9 : 1	2·4 : 1	5·9 : 1	—	—	Dentate pecten on apex leg 4
C. alatus Heegaard, 1943	0·8 : 1	1·1 : 1	3·2 : 1	4·8 : 1	—	—	POP tine-like
C. amblygenitalis Pillai, 1961	1·6 : 1	2·1 : 1	2·6 : 1	3·0 : 1	—	—	Large posterior lobes on GC
C. antennatus sp. nov.	0·9 : 1	0·9 : 1	4·1 : 1	8·8 : 1	4·5 : 1	1 : 3·2	See below
C. brevis Shiino, 1954	0·8 : 1	1·2 : 1	2·5 : 1	6·7 : 1	7·6 : 1	1 : 3·3	—
C. calotomi Shiino, 1954	0·7 : 1	1·1 : 1	2·0 : 1	6·7 : 1	—	—	Spine 1 on leg 1 absent
C. eventilis Leigh-Sharpe, 1934	0·6 : 1	0·5 : 1	3·0 : 1	8·0 : 1	—	—	—
C. fistulariae Yamaguti, 1936	1·4 : 1	1·1 : 1	3·0 : 1	4·7 : 1	4·4 : 1	1 : 2·8	—
C. flexispina Lewis, 1964	0·9 : 1	1·0 : 1	3·3 : 1	7·5 : 1	6·6 : 1	1 : 2·0	—
C. hamruri Pillai, 1964	0·9 : 1	2·1 : 1	2·0 : 1	2·9 : 1	—	—	Myxal process on ♀ MXP
C. kalumai Lewis, 1964	0·8 : 1	1·0 : 1	3·6 : 1	7·0 : 1	—	—	—
C. klawei Shiino, 1959	1·3 : 1	0·9 : 1	4·4 : 1	4·3 : 1	—	—	GC longer than DS
C. longiabdominis Shiino, 1965	1·2 : 1	2·5 : 1	1·0 : 1	1·8 : 1	2·6 : 1	1 : 2·6	—
C. longicaudatus Brady, 1899	—	—	—	—	4·2 : 1	1 : 1·7	Mx2 margin serrated
C. longipedis Bassett-Smith, 1898	0·9 : 1	1·2 : 1	2·0 : 1	5·6 : 1	5·7 : 1	1 : 1·4	Mx2 margin serrated
C. macarovi Gussev, 1951	1·0 : 1	1·9 : 1	1·3 : 1	2·5 : 1	3·0 : 1	1 : 2·5	Mx2 margin serrated
C. orientalis Gussev, 1951	0·9 : 1	0·6 : 1	2·8 : 1	4·8 : 1	—	—	Dentate pecten on apex leg 4
C. oviceps Shiino, 1952	0·8 : 1	1·1 : 1	2·7 : 1	7·7 : 1	4·9 : 1	1 : 1·9	—
C. polycanthi Gnanamuthu, 1950	0·8 : 1	0·9 : 1	2·4 : 1	4·6 : 1	5·7 : 1	1 : 6·0	POP tine-like
C. pseudokalumai Lewis, 1968	0·9 : 1	0·6 : 1	4·3 : 1	10·7 : 1	—	—	—
C. punctatus Shiino, 1955	0·9 : 1	1·0 : 1	3·0 : 1	6·2 : 1	6·5 : 1	1 : 2·1	—
C. rugosus Shiino, 1959	0·9 : 1	1·1 : 1	2·8 : 1	5·9 : 1	—	—	Mx2 margin serrated
C. scabiei Gnanamuthu, 1950	0·9 : 1	1·1 : 1	1·7 : 1	5·1 : 1	—	—	Mx2 margin serrated
C. sensilis Kabata & Gusev, 1966	0·9 : 1	1·0 : 1	2·3 : 1	5·9 : 1	—	1 : 4·0	3 setae on inner process leg 5
C. sibogae sp. nov.	1·3 : 1	1·8 : 1	0·9 : 1	2·7 : 1	3·4 : 1	1 : 2·0	Mx2 margin serrated
C. tenuicaudatus Shiino, 1959	1·2 : 1	2·4 : 1	1·1 : 1	2·2 : 1	—	—	CR 4·5 times longer than wide
C. thyrsitae Kazachenko, Korotaeva & Kurochkin, 1972	1·1 : 1	2·0 : 1	1·2 : 1	2·2 : 1	—	—	Mx2 margin serrated
C. triangularis Shiino, 1954	1·0 : 1	1·4 : 1	2·5 : 1	3·9 : 1	4·4 : 1	1 : 4·0	—

Abbreviations: GCL genital complex length, GCW genital complex width, ABL abdomen length, DSL dorsal shield length, ABL1 length of abdomen segment 1, ABL2 length of abdomen segment 2, POP post oral process, MXP maxilliped, Mx2 second maxilla, CR caudal rami.

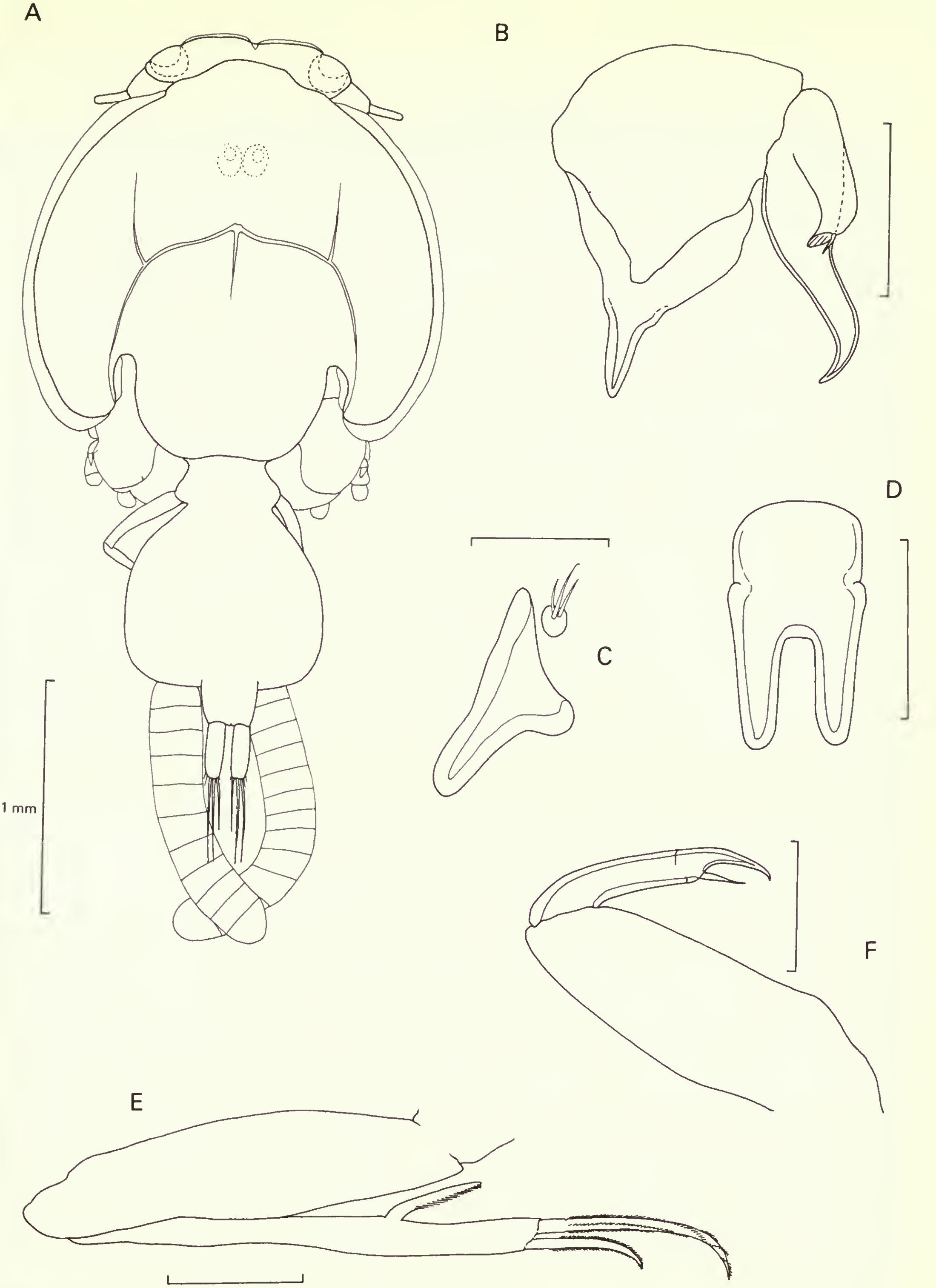

Fig. 8 *Caligus antennatus* sp. nov. paratype ♀. A, dorsal; B, second antenna, ventral; C, first maxilla, ventral; D, sternal furca, antero-ventral; E, second maxilla, anterior; F, maxilliped, posterior. Scales 100 μm unless otherwise stated.

with maximum width in posterior third and tapering anteriorly. Abdomen 1-segmented and broader than long. Caudal rami (Fig. 9B) about 2·5 times longer than wide and armed with 3 long plumose setae and 3 short setae. Body length of females ranging from 2·8 to 3·4 mm, with a mean of 3·1 mm (based on 30 specimens).

First antenna of usual form for genus. Second antenna (Fig. 8B) with posteriorly directed spinous process on basal segment; middle segment unarmed; terminal segment claw-like and with a large conical process proximally on ventral surface; conical process with concave tip striated internally and with a small seta subapically. Post antennal process as in male. Mandible of usual structure for genus. First maxilla (Fig. 8C) anterior process with 3 naked setae, posterior process with a simple tine. Second maxilla (Fig. 8E) with long flabellum on brachium: calamus nearly twice as long as canna and bearing 4 strips of serrated membrane running obliquely along its length; canna with bilateral serrated membranes. Maxilliped (Fig. 8F) with slender unarmed basal segment and terminal claw bearing a single seta on concave margin near tip. Sternal furca (Fig. 8D) small with parallel tines.

Leg 1 (Fig. 9A) with characteristic structure of *macarovi*-group: exopod segment 2 with 3 long setae on posterior margin, each with a plumose medial margin and with long pinnules on proximal quarter of outer margin and a row of fine short pinnules resembling a striated membrane in appearance on the distal three quarters of the outer margin. Distal margin with 4 elements (Fig. 9C); spine 1 simple, spines 2 and 3 each with an accessory process extending beyond its tip, seta 4 long, unilaterally pinnate and situated ventral to distal margin. Leg 2 (Fig. 9D) endopod segments 1 and 2 with pinnule rows along outer margins: exopod segments 1 and 2 with large spines at outer distal angles directed obliquely over ventral surface of ramus; segment 3 with 1 outer margin spine armed with smooth membrane unilaterally, an apical seta and 5 plumose setae on inner margin. Leg 3 (Fig. 10A) of usual structure for genus. Leg 4 (Fig. 10C) 3-segmented; second segment with a long apical spine, third segment with 3 distal spines (Fig. 10B), each with a pecten at its base and with 1 or 2 rows of minute pinnules. Leg 5 (Fig. 10E) situated postero-laterally on ventral surface of genital complex, comprising an inner process bearing 2 plumose setae and an outer process bearing a single seta. Leg 6 probably represented by a flattened plate with fine surface striations.

ADULT MALE. Dorsal shield (Fig. 11A) as in female but with relatively wider posterior sinuses. Genital complex wider than long, with greatest width about midpoint. Abdomen (Fig. 11B) 2-segmented, just longer than wide; second segment about 3 times longer than first. Caudal rami about 4·4 times longer than wide, plumose on medial margin and bearing 3 short setae and 3 long distal setae, innermost distal seta plumose medially and with short pinnules laterally as on remaining 2 distal setae. Appendages as in female except second antenna, first maxilla, maxilliped and legs 5 and 6. Second antenna (Fig. 10D) 3-segmented; basal segment elongate and with a single raised adhesion pad; middle segment robust, tapering distally and bearing irregular adhesion pads proximally and a raised adhesion pad distally; third segment (Fig. 10G) with spatulate apex subdivided distally and armed with 2 naked setae. Post antennal process (Fig. 10F) with a slender tine and 2 simple setules on basal portion. Post oral process (Fig. 10H) comprising a conical swelling with surface striations. Tine of first maxilla (Fig. 11D) with small subapical nodule on ventral surface. Maxilliped (Fig. 11E) with robust basal segment, swollen proximally on myxal surface and with a small nodular myxal process distally; terminal claw as in female but with additional small process proximally on concave margin. Leg 5 (Fig. 11C) positioned laterally on genital complex and comprising an inner process bearing 2 plumose setae and an outer process bearing 1 seta. Leg 6 represented by a single process bearing 1 plumose seta apically. Body length of males ranging from 2·7 to 4·2 mm, with a mean of 3·1 mm (based on 33 specimens).

MATERIAL EXAMINED. Holotype ♀, 29 ♀♀ paratypes, 33 ♂♂ paratypes, 1 ♀ and 1 ♂ in amplexus and 11 developmental stages: from body surface of *Acanthopagrus latus* (Houttuyn) held in culture tanks at the Fishery Station, Raas, Kuwait. Collected and presented by Dr I. U.

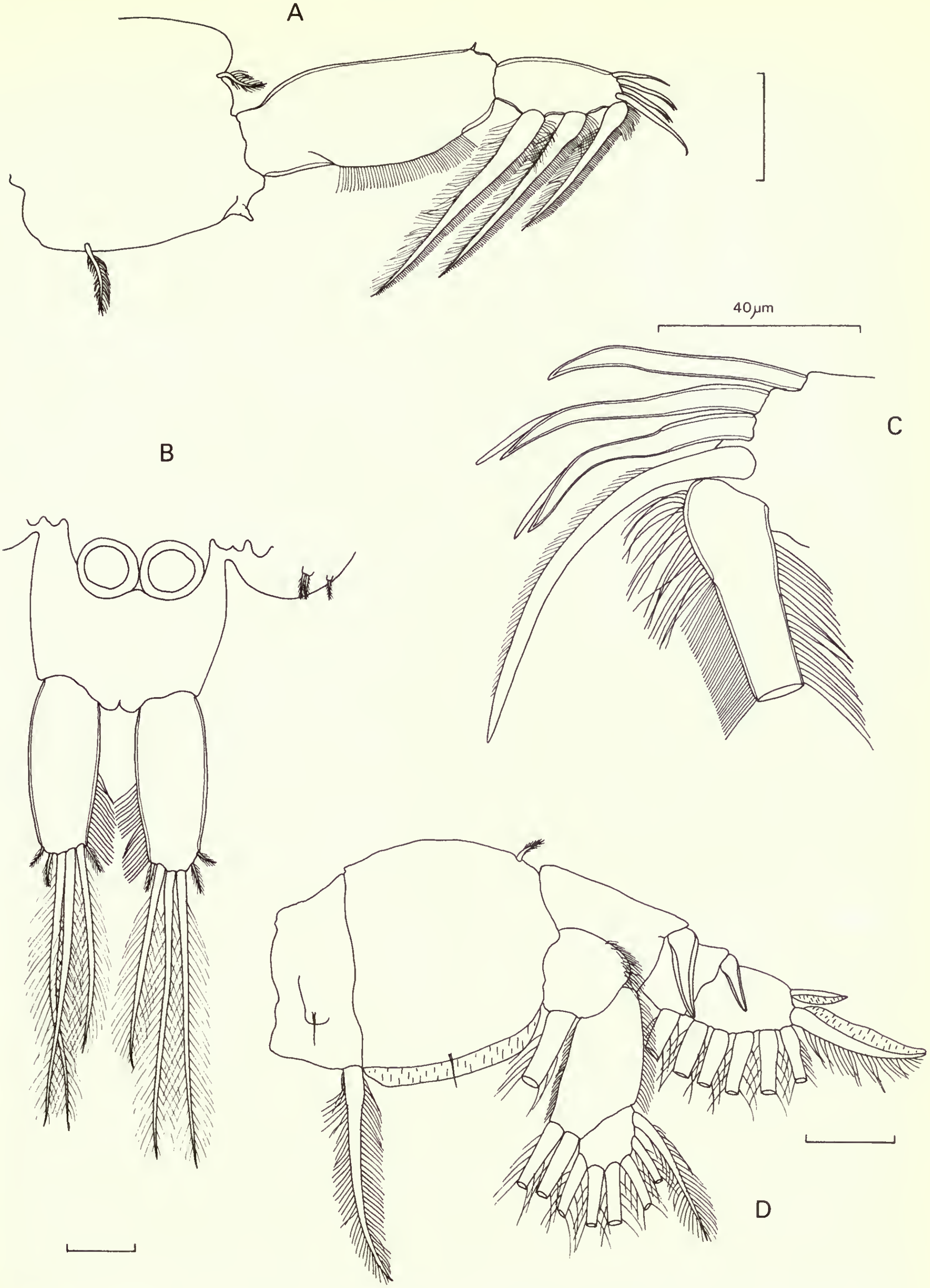

Fig. 9 *Caligus antennatus* sp. nov. paratype ♀. A, leg 1, ventral; B, abdomen, ventral; C, tip of exopod of leg 1, ventral; D, leg 2, ventral. Scales 100 µm.

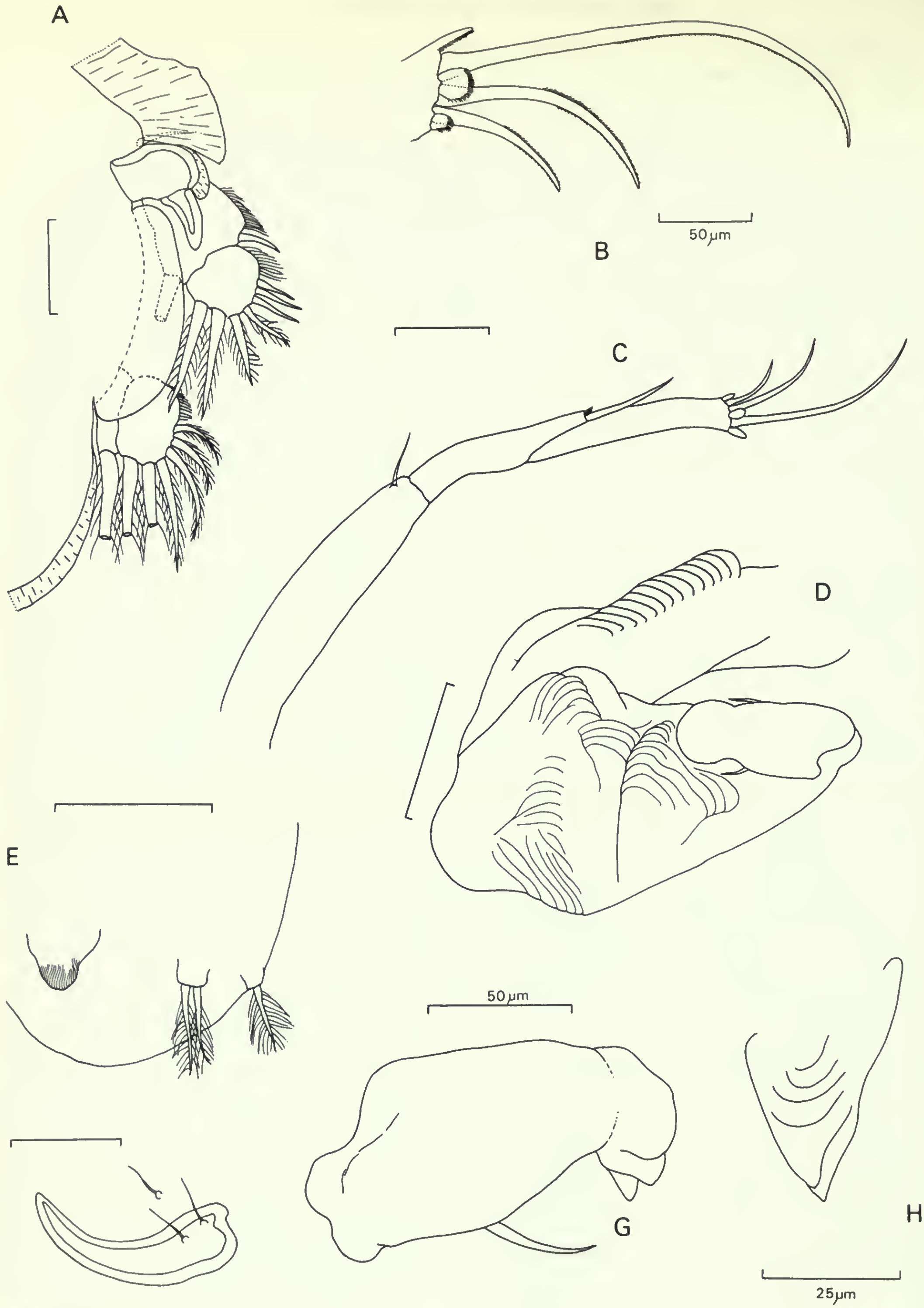

Fig. 10 *Caligus antennatus* sp. nov. paratypes ♀ and ♂. A, ♀ leg 3 rami, ventral; B, tip of leg 4, ventral; C, leg 4, ventral; D, ♂ second antenna, postero-ventral; E, ♀ leg 5, ventral; F, ♂ post antennal process, ventral; G, tip of second antenna, posterior; H, post oral process, ventral. Scales 100 µm unless otherwise stated.

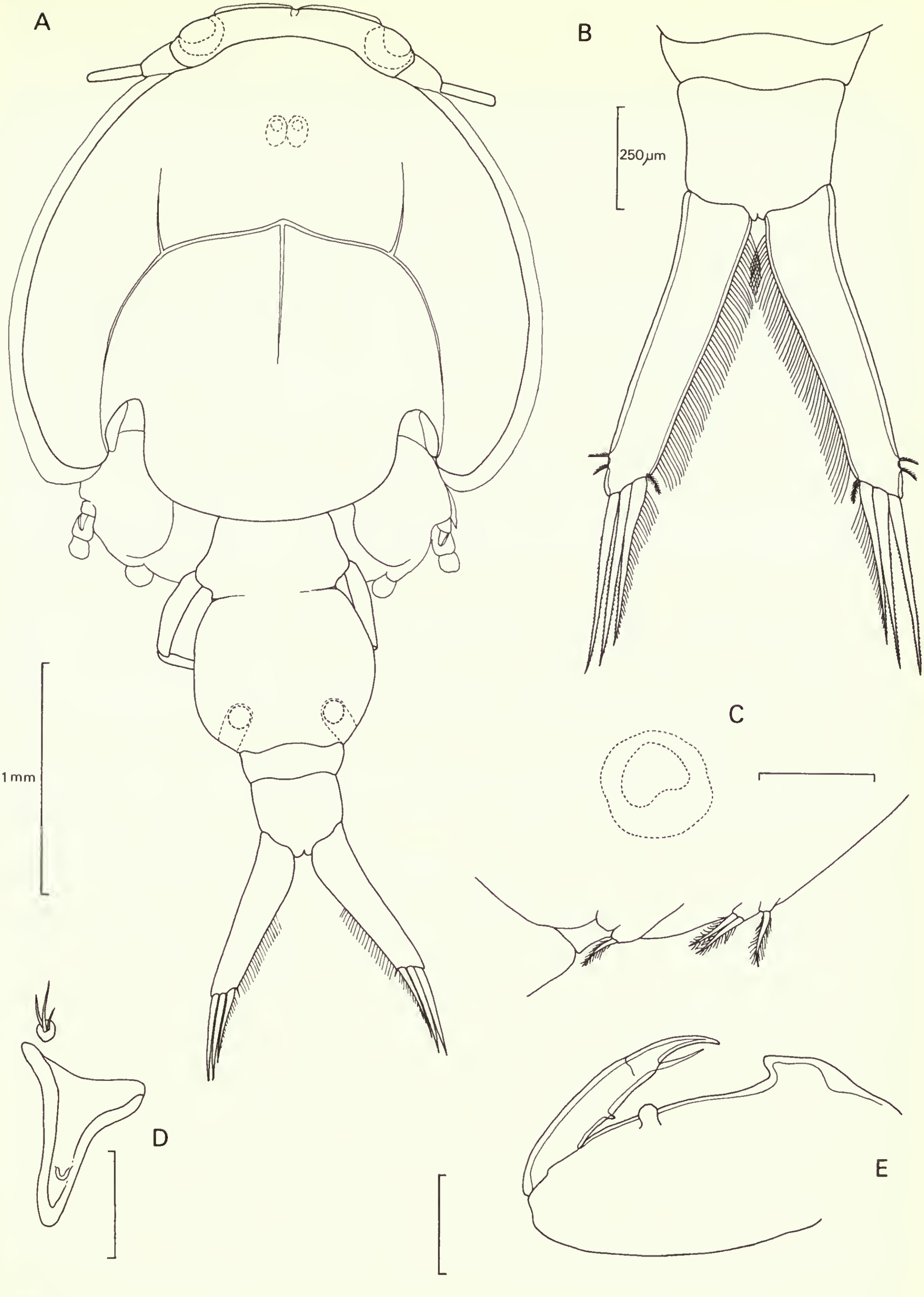

Fig. 11 *Caligus antennatus* sp. nov. paratype ♂. A, dorsal; B, abdomen, ventral; C, legs 5 and 6, ventral; D, first maxilla, ventral; E, maxilliped, posterior. Scales 100 µm unless otherwise stated.

Tareen. B.M.(N.H.) 1979.1113 (Holotype ♀), 1979.1114–1143 (Paratype ♀♀), 1979.1144–1176 (Paratype ♂♂) and 1979.1177–1187 (couple in amplexus and developmental stages).

REMARKS. *C. antennatus sp. nov.* can be placed in the *macarovi*-group as it exhibits the characteristic structure and armature of the maxillipeds, legs 1 and 4 and the male abdomen. It differs from all other species in the group in the possession of a large conical process on the third segment of the second antenna in the female and in the nature of the caudal rami in the male. These two unique characters also serve to distinguish *C. antennatus sp. nov.* from all other *Caligus* species, except *C. hottentotus* Barnard, 1955. Barnard's (1955) description of *C. hottentotus* was incomplete but the general form of the genital complex and abdomen in both sexes is similar to that of *C. antennatus*. The differences between the two species are body size, the marked tapering of the abdomen in the female of *C. hottentotus,* the shape of the sternal furca, the length to width ratio of the male genital complex (which is longer than wide in *C. hottentotus* and wider than long in *C. antennatus*) and the relative lengths of the caudal rami and abdomen in the male (the caudal rami are 1·7 times longer than the abdomen in *C. antennatus* and 2·5 times longer in *C. hottentotus*).

Acknowledgements

We would like to thank Dr S. Pinkster of the Zoölogisch Museum, Amsterdam for arranging the loan of Leigh-Sharpe's *C. dubius* material from the Siboga expedition collection. We are also most grateful to Dr Ray Ingle for reading and commenting on the manuscript.

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A revision of the spider genus *Onomastus* (Araneae: Salticidae)

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Introduction

Onomastus Simon, 1900 is a small genus of spiders presently classified in the salticid subfamily Lyssomaninae. It is comprised of four known species, *O. complexipalpis* sp. n., from Borneo, *O. patellaris* Simon from India, *O. quinquenotatus* Simon and *O. nigricauda* Simon, the type species, from Sri Lanka.

Most species are small (2·0 to 4·0 mm total length) and whitish to pale yellow when preserved in spirit. They resemble lyssomanines in their colouration, general slender habitus and by having the eyes arranged in four transverse rows. Nevertheless, the structure of the genitalia shows that they are not closely related to either new or old world lyssomanines. They are however, of special interest as the male palps are unusually complex. In contrast the female epigynes are apparently simple in structure and similar in form. Unfortunately they are poorly defined and precise details cannot easily be resolved. It is to be regretted that specimens seem to be rare in museum collections as only type material was available for study. Their biology is unknown.

In the present paper the genus is redefined and its affinities discussed, four species are described, one of which is new, an identification key is provided and three lectotypes newly designated. The measurements were made in the manner described by Wanless (1978), but for the leg spination the system adopted is that used by Platnick and Shadab (1975).

Genus *Onomastus* Simon

Onomastus Simon, 1900 : 29. Type species *Onomastus nigricauda* Simon, by original designation. Simon, 1901 : 395, 398, 400. Petrunkevitch, 1928 : 181 Roewer, 1954 : 932. Bonnet, 1958 : 3185.

DEFINITION. Small to medium spiders ranging from about 3·0 to 4·5 mm in length. Sexual dimorphism sometimes evident in colour markings; specimens preserved in spirit (75 per cent alcohol) generally pale yellow to whitish yellow; not hirsute. *Carapace*: moderately high, longer than broad, widest at posterior margin of coxae II; fovea indistinct, of medium length, situated more or less midway between posterior lateral eyes and posterior margin of thorax; sculpturing not marked. *Eyes*: with black surrounds except anterior medians; set on low tubercles; arranged in four transverse rows comprised of anterior medians, anterior laterals, posterior medians and posterior laterals; anterior medians largest, more or less contiguous, occupying almost full breadth of facies; anterior laterals more than half diameter of anterior medians, positioned just behind and plainly wider than first row; posterior medians minute, closer to and positioned on or slightly inside optical axis of anterior laterals; posterior laterals as large or almost as large as anterior laterals, set closer together and well inside lateral margins of carapace; quadrangle formed by posterior median and posterior lateral eyes broader than long; entire quadrangle (measured from base of anterior medians to posterior margin of posterior laterals) occupying between 35 and 42 per cent of carapace length. *Clypeus*: between 20 and 60 per cent of diameter of anterior median eyes; sometimes clothed in recumbent shining white hairs layered perpendicularly. *Chelicerae*: small to

Bull. Br. Mus. nat. Hist. (Zool.) **39** (3) : 179–188 Issued 27 November 1980

medium, more or less vertical or posteriorly inclined; generally parallel; promargin with three to four teeth, retromargin with seven or eight. *Maxillae*: of medium length, subparallel with scopula. *Labium*: about as wide as long, subtriangular. *Sternum*: broadly scutiform, margins generally ill-defined. *Pedicel*: short. *Abdomen*: elongate ovoid, sometimes tapered; spinnerets moderately long, posteriors slightly longer than the rest, anteriors robust, medians and posteriors slender; tracheal system not examined (insufficient material); position of colulus sometimes indicated by two or three fine setae (lacking or rubbed in majority of specimens); anal tubercle a moderately well developed cone. *Legs*: long and slender; fringes absent; spines long and moderately robust, rather pale; claws pectinate; tufts present; scopulae lacking. *Female palps*: long and slender with apical claw and whorl of six or seven spines in proximal half of tarsi. *Male palps*: complex and interspecifically distinct. Femora unmodified (i.e. lacking vetral furrow and distal apophysis found in *Asemonea* O. P.-Cambridge and *Pandisus* Simon); patellae with broad retrolateral apophyses; tibiae without retrolateral apophyses; cymbium with short to moderately long distal finger-like extension, sometimes with basal retromarginal protuberance, fringed in long fine hairs (not included in the figures); embolus (e) moderately long and slender to exceedingly long and thread-like, originating (oe) from tegulum within alveola cavity; tegulum (st) irregular in outline with sinuous ducts, sometimes obscured by conductor, apophyses usually present, apophysis (y) characteristic of genus; conductor (c) arising from tegulum, extremely variable, scalloped or grooved on peripheral margin to form an embolic guide (eg) which terminates in a spur (s); secondary conductor lacking; median apophysis (ma) also a tegular process variable in shape, branched and heavily sclerotized, lobe-like or slender and curved, appearing to embrace and protect the conductor spur. *Epigynes:* small and indistinct; openings paired, ducts evidently lacking; spermathecae relatively large.

AFFINITIES AND DIAGNOSIS. The disposition of the eyes, position of the fovea and general habitus suggest that *Onomastus* may belong in the subfamily Lyssomaninae as defined by Galiano (1976). The genus is not, however, closely related to either new or old world genera and I am unable to detect any synapomorphies (shared, uniquely derived characters). At present, the subfamily would appear to represent a polyphyletic group that will have to be reclassified when related genera have been revised. For the moment I do not intend to propose formal nomenclatorial changes.

Onomastus is readily distinguished from other lyssomanine genera by the eye pattern, the indistinct fovea, the presence of the palpal subtegular apophysis (y) (Fig. 3E) in males and the apparent absence of epigynal ducts in females (Fig. 2E).

REMARKS. Out-group comparison of the male palps of *Onomastus* with those of *Oxyopes* (family Oxyopidae) has revealed superficial similarities in structure which are worth noting. For example in *Oxyopes javanus* Thorell, the embolus rests in a grooved conductor which terminates in a spur that is protected and partly supported by a heavily sclerotized median apophysis; also protecting the spur and embolic tip is a secondary membranous conductor, lacking in *Onomastus,* but evidently present in *Lyssomanes* Hentz (see Galiano 1962). Lehtinen (1975) considers that the similarity of hair ultra structure in the Salticidae and Oxyopidae clearly demonstrates the close relationship of the two families. If this is correct then these tentative observations may be significant as they suggest that *Onomastus* may be primitive and that the palps have retained several characters (eg, conductor and median apophysis) which have been secondarily reduced in the majority of Salticidae.

List of species in the genus *Onomastus* Simon, 1900

Onomastus complexipalpis sp. n.
O. nigricauda Simon, 1900
O. patellaris Simon, 1900
O. quinquenotatus Simon, 1900

Key to species of *Onomastus*

Males (male of *quinquenotatus* unknown)

1 Conductor extremely large (Fig. 4E) (Borneo) . . . . ***COMPLEXIPALPIS*** sp. n. (p. 187)
– Conductor small (India & Sri Lanka) 2
2 Tegulum with distinctive apophysis (x) (Fig. 3B, E, G) . . . ***PATELLARIS*** Simon (p. 183)
– Tegulum without distinctive apophysis (x) (Fig. 1C, F, G) ***NIGRICAUDA*** Simon (p. 181)

Females (female of *complexipalpis* unknown)

1 Abdomen with pattern of black spots; apices of tibiae with black markings; epigyne as in Fig. 2C, D (Sri Lanka) . . . . ***QUINQUENOTATUS*** Simon (p. 183)
– Abdomen and leg markings apparently lacking; epigyne otherwise 2
2 Epigyne lightly sclerotized with oblique dark bars (Fig. 3C) (India) ***PATELLARIS*** Simon (p. 183)
– Epigyne heavily sclerotized with inverted dark U-shaped bars (Fig. 1D) (Sri Lanka) ***NIGRICAUDA*** Simon (p. 181)

Onomastus nigricauda Simon
(Fig. 1A-G)

Onomastus nigricanda Simon, 1900 : 29 [lapsus calami].
O. nigricauda Simon, 1900 : 29, ♂. LECTOTYPE ♂ (here designated) Sri Lanka, Galle, (MNHN, Paris, 20404). Simon, 1901 : 391, 396, 400. Petrunkevitch, 1928 : 181. Roewer, 1954 : 932.
O. nigricaudus: Bonnet, 1958 : 3186 [unjustified emendation].

DIAGNOSIS. *O. nigricauda* seems to be most closely related to *O. patellaris* but may be easily distinguished by the structure of the palp (Fig. 1C, F, G) in males; females are separated with more difficulty by the inverted u-shaped epigynal bars (Fig. 1D, E).

MALE LECTOTYPE. *Carapace* (Fig. 1A, B): pale amber with whitish yellow eye region. *Eyes*: with black surrounds except AM; fringed in shining white hairs. *Clypeus*: thinly clothed in fine shining hairs. *Chelicerae*: small; pale yellow, shiny; teeth not examined. *Maxillae and labium*: pale yellow. *Sternum*: whitish yellow. *Coxae*: subequal; pale yellow. *Abdomen*: whitish yellow; anterior and posterior spinnerets blackish, medians whitish yellow. *Legs*: pale yellow; spines very pale; spination of legs I: metatarsi V 4–0–0, P 1–1–0, R 1–1–0; tibiae V 2–4–2, P 1–0–1, R 1–0–1, D 1–0–1; patellae P 0–1–0, R 0–1–0; femora P 0–0–1, D 1–1–1, R 0–1–1. *Palp* (Fig. 1C, F, G): cymbium slightly produced basally; embolus (e) long and slender, originating within alveolar cavity and retained in the heavily sclerotized embolic guide (eg), proximal limit of which is indicated by a small flange (f); median apophysis (ma) branched, heavily sclerotized.

Dimensions (mm): total length 3·2; carapace length 1·52, breadth 1·2, height 0·74; abdomen length 1·64; eyes, AM row 0·8, AL row 1·1, PM row 0·76, PL row 0·77; quadrangle length 0·68. *Ratios*: AM : AL : PM : PL : 10·5 : 6 : 1 : 5; AL—PM—PL : 5—3; AM : CL (clypeus) : 10·5 : 2.

FEMALE FROM SRI LANKA (formerly undescribed). Similar to ♂ except for the following. *Carapace*: pale yellow grading to whitish yellow in eye region. *Clypeus*: thickly clothed in shining white hairs. *Abdomen*: whitish yellow; spinnerets pale yellow. Spination of legs I: metatarsi V 4–2–0, P 1–0–0 R 1–0–0; tibiae V 4–4–4, D 0–1–0; femora P 0–0–1, D 1–1–1, R 0–0–1. *Epigyne* (Fig. 1D, E): small and dark.

Dimensions (mm): total length 4·3; carapace length 1·52, breadth 1·12, height 0·76; abdomen length 1·88; eyes, AM row 0·8, AL row 1·12, PM row 0·76, PL row 0·8; quadrangle length 0·64. *Ratios:* AM : AL : PM : PL : 10·5 : 6 : 1 : 5; AL—PM—PL : 3—6; AM : CL : 10·5 : 2.

VARIATION. Another ♀ from Sri Lanka 3·48 mm total length, 1·48 mm carapace length.

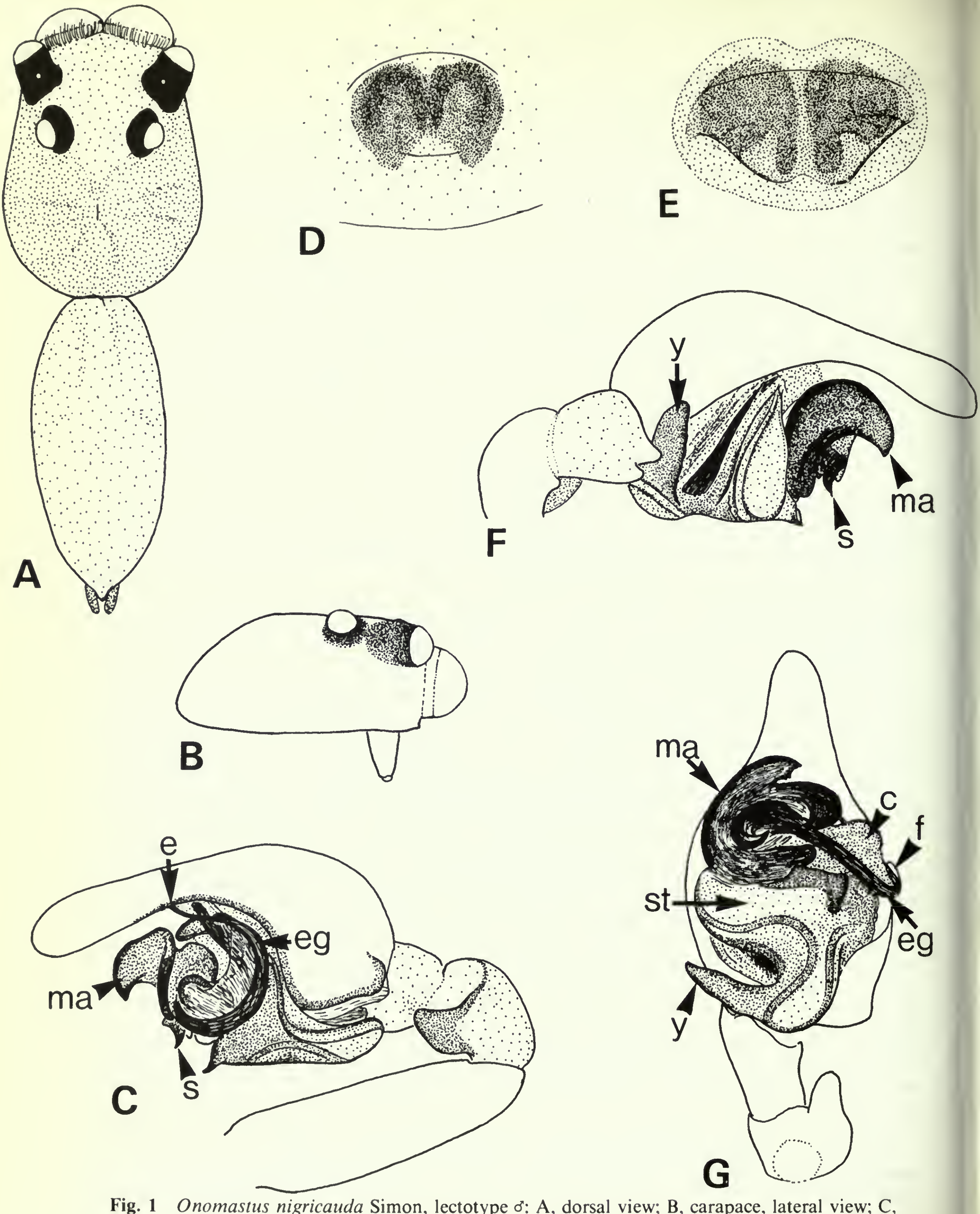
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Fig. 1 *Onomastus nigricauda* Simon, lectotype ♂: A, dorsal view; B, carapace, lateral view; C, palp, retrolateral view; F, palp, prolateral view; G, palp, ventral view. ♀ from Sri Lanka: D, epigyne; E, vulva, ventral view.

DISTRIBUTION. Sri Lanka.

MATERIAL EXAMINED. Lectotype ♂, data as given in synonymy. Sri Lanka: Galle, 2 ♀♀ (*E. Simon*) (MHN, Paris, 204004).

Onomastus quinquenotatus Simon
(Fig. 2A-E)

Onomastus quinquenotatus Simon, 1900 : 29, ♀. LECTOTYPE ♀ (here designated) Sri Lanka (MNHN, Paris, 20377) [Examined]. Roewer, 1954 : 932. Bonnet, 1958 : 3186.

DIAGNOSIS. *O. quinquenotatus*, known only from the female seems to be most closely related to *O. nigricauda* Simon and *O. patellaris* Simon, but may be separated by the abdominal markings (Fig. 2A) and the shape of the epigynal opening, especially when viewed slightly from behind (Fig. 2C).

MALE. Unknown.

FEMALE PARALECTOTYPE. *Carapace* (Fig. 2A, B): pale yellow with lighter eye region. *Eyes*: with black surrounds except AM; fringed in silky white hairs. *Clypeus*: clothed in fine weakly iridescent hairs. *Chelicerae*: pale yellow; promargin with 3 or 4 minute teeth difficult to see, retromargin with 7 or 8 forming a minute serrated ridge. *Maxillae and labium*: pale yellow. *Sternum*: whitish yellow. *Coxae*: subequal; whitish yellow. *Abdomen*: pale yellow with 5 black spots; spinnerets pale yellow. *Legs*: pale yellow with conspicuous black wedge-shaped lateral markings on apices of tibiae I-IV, patellae I (retrolateral only) and femora I (retrolateral only); spines long and slender, rather pale and less numerous on legs III-IV. Spination of legs I: metatarsi V 2–2–0, P 1–0–1, R 1–0–1; tibiae V 4–4–4, D 0–1–0, femora P 0–0–1, D 1–1–1, R 0–0–1. *Palp*: pale yellow. *Epigyne* (Fig. 2C–E): dark redbrown, small and poorly defined, the opening is clearer when viewed from slightly behind.

Dimensions (mm): total length 3·6; carapace length 1·58, breadth 1·2, height 0·63; abdomen length 2·08; eyes, AM row 0·76, AL row 0·96, PM row 0·71, PL row 0·72; quadrangle length 0·56. *Ratios*: AM : AL : PM : PL 9 : 5 1 4; AL—PM—PL : 2·5—5; AM : CL : 9 : 3

VARIATION. ♀ lectotype 3·8 mm total length, 1·56 mm carapace length. The abdominal spots are pale and only three are evident.

DISTRIBUTION. Sri Lanka.

MATERIAL EXAMINED. Lectotype ♀, paralectotype ♀, data as given in synonymy. In the original description Simon gives Columbo and Kandy as the localities, but he did not record which specimen came from which area.

Onomastus patellaris Simon
(Fig. 3A-G)

Onomastus patellaris Simon, 1900 : 29, ♂. LECTOTYPE ♂ (here designated) India, Kodaikanal, Madras, (MNHN, Paris, 14858) [Examined]. Simon, 1901 : 395, 396. Roewer, 1954 : 932. Bonnet, 1958 : 3186.

DIAGNOSIS. *O. patellaris* seems to be most closely related to *O. nigricauda* but may be readily distinguished by the structure of the palp in males (Fig. 3B, E, G) and with more difficulty by the oblique epigynal bars in females (Fig. 3C).

MALE LECTOTYPE. *Carapace* (Fig. 3A, F): pale yellow with whitish yellow eye region. *Eyes*: with black surrounds except AM; fringed in silky white hairs. *Clypeus*: hairs evidently lacking (?rubbed). *Chelicerae*: medium size; pale yellow; teeth not examined. *Maxillae and* *labium*: whitish yellow. *Sternum*: whitish yellow. *Coxae*: subequal; pale yellow. *Abdomen*: whitish yellow. *Legs*: whitish yellow; spines long and slender, almost translucent. Spination of legs I: metatarsi V 2–2–0, P 1–0–1, R 1–0–1; tibiae V 2–4–2, P 1–0–1, R 2–0–1, D 1–0–1; patellae P 0–1–0, R 0–1–0; femora spines evidently lacking. *Palp* (Fig. 3B, E, G): embolus (e) moderately long, detached from embolic guide, its origin (oe) not completely obscured by lobe-like median apophysis; tegulum (st) with several apophyses, (x) diagnostic for males.

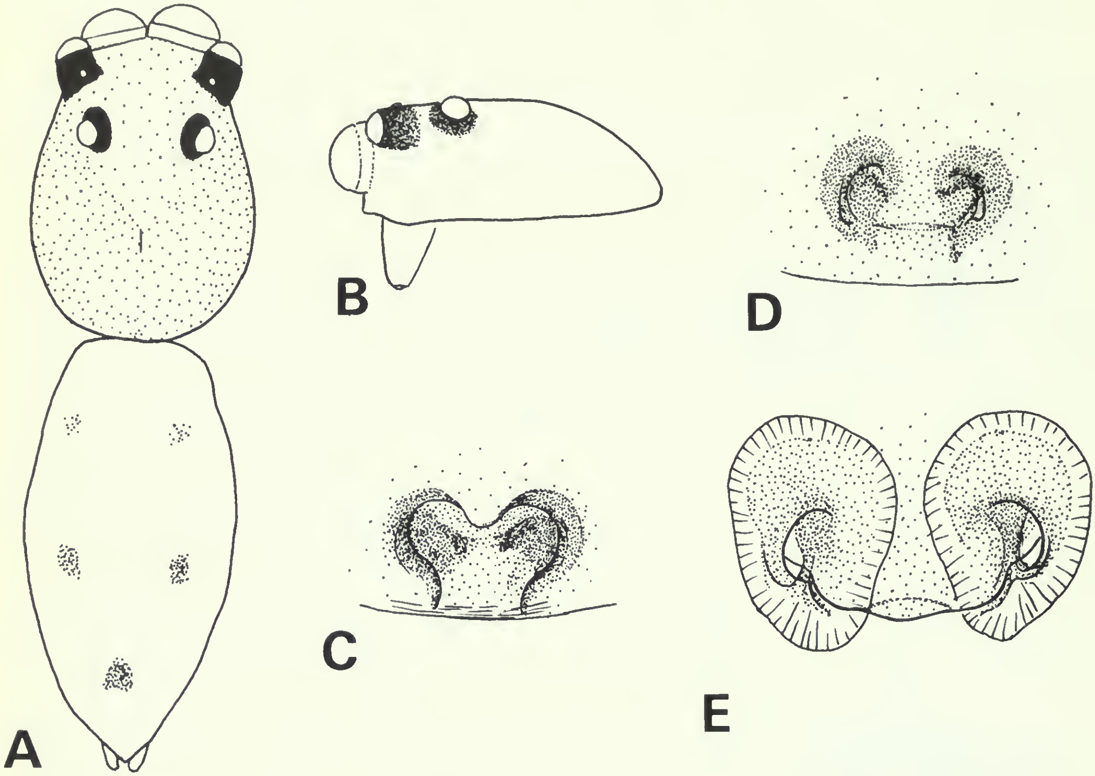

Fig. 2 *Onomastus quinquenotatus* Simon, paralectotype ♀: A, dorsal view; B, carapace, lateral view; C, epigyne, viewed slightly from behind; D, epigyne, ventral view; E, vulva, ventral view.

Dimensions (mm): total length 3·88; carapace length 1·72, breadth 1·32, height 0·86; abdomen length 2·08; eyes, AM row 0·8, AL row 1·04, PM row 0·78, PL row 0·84; quadrangle length 0·64. *Ratios*: AM : AL : PM : PL : 10 : 5 : 1 : 5; AL—PM—PL : 3—6; AM : CL : 3 : 6.

Female from madras, india (formerly undescribed). Similar to ♂ except for the following. *Clypeus*: clothed in shining white hairs. *Chelicerae*: promargin with 5 minute teeth, retromargin with 7. *Legs*: spination of legs I: metatarsi V 2–2–0, P 1–0–1, R 1–0–1; tibiae V 4–4–2, P 1–0–1, R 1–0–1, D 0–1–0; patellae P 0–1–0, R 0–1–0; femora P 0–0–1, D 1–1–1. *Epigyne* (Fig. 3C, D): small; orange-brown with darker oblique bars.

Dimensions (mm): total length 4·16; carapace length 1·68, breadth 1·22, height 0·72; abdomen length 2·48; eyes, AM row 0·82, AL row 1·03, PM row 0·76, PL row 0·77; quadrangle length 0·6. *Ratios*: AM : AL : PM : PL : 10 : 5 : 0·8 : 4·2; AL—PM—PL : 3—6; AM : CL : 10 : 3.

Variation. ♀ total length 4·16 to 4·4 mm, carapace length 1·64–1·72 mm (4 specimens). The epigynes are often plugged, but the oblique dark bars can usually be distinguished.

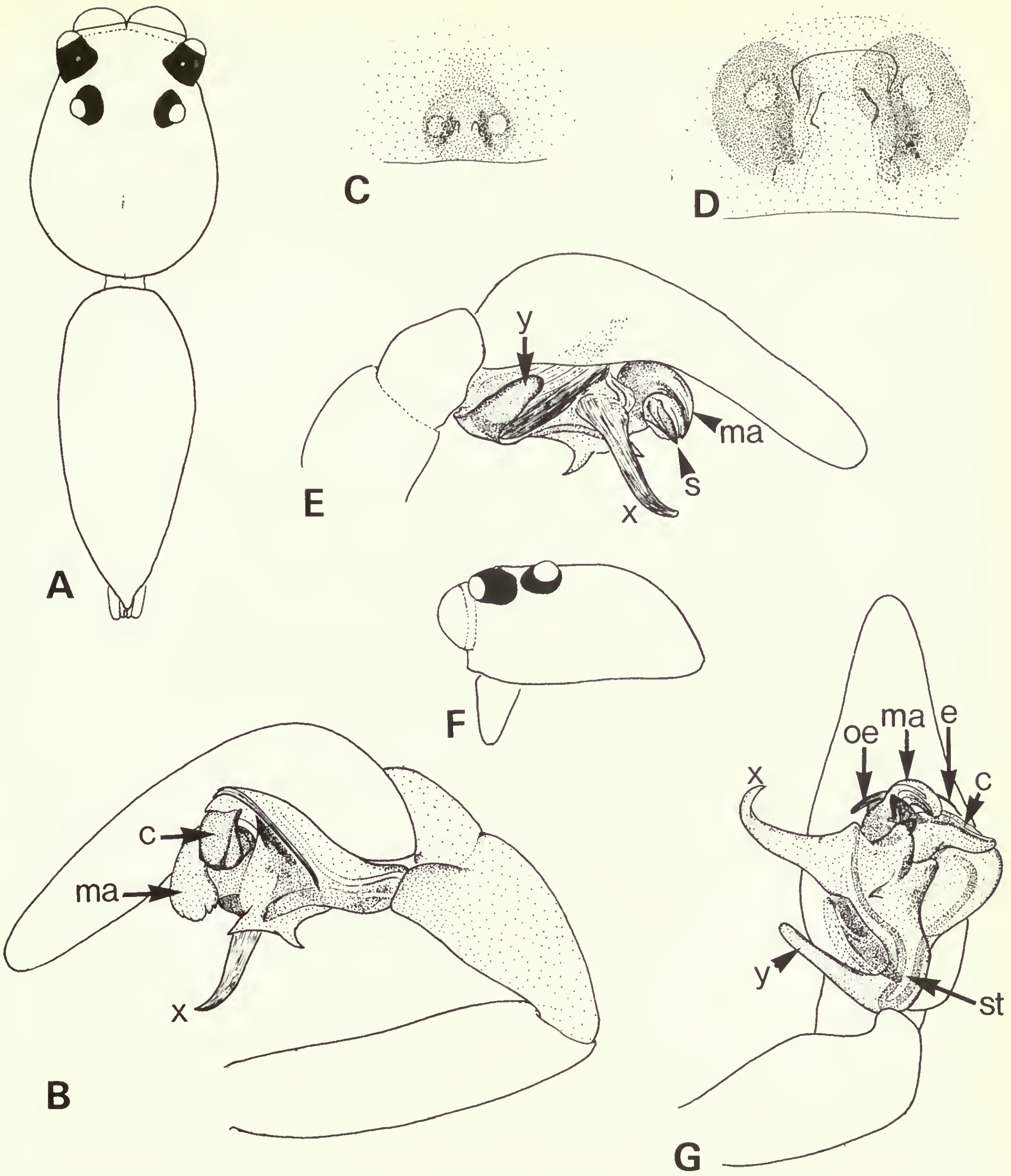
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Fig. 3 *Onomastus patellaris* Simon, lectotype ♂: A, dorsal view; B, palp, retrolateral view; E, palp, prolateral view; F, carapace, lateral view; G, palp, ventral view. ♀ from Madras: C, epigyne; D, vulva, ventral view.

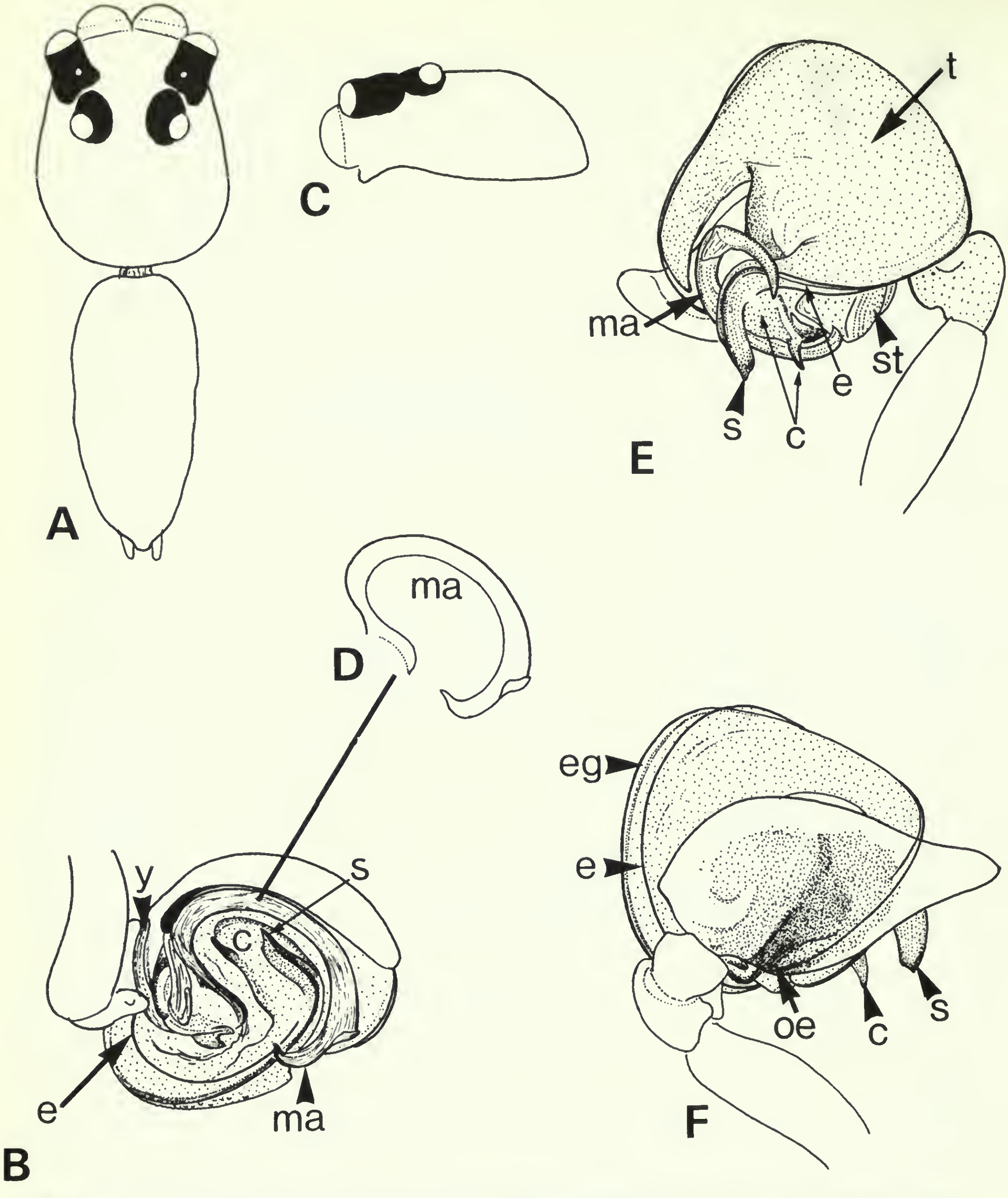
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Fig. 4 *Onomastus complexipalpis* sp. n., holotype ♂: A, dorsal view; B, palp, retrolateral view; C, carapace, lateral view; D, profile of median apophysis; E, palp, ventral view; F, palp, dorsal view.

DISTRIBUTION. India.

MATERIAL EXAMINED. Lectotype ♂, data as given in synonymy. India: Trichinopoly, Madras, 4 ♀♀, (*R. P. Malat*) (MNHN, Paris, 14898).

Onomastus complexipalpis sp. n.

(Fig. 4A-F)

DIAGNOSIS. *O. complexipalpis* is a distinctive species easily distinguished from other known species of *Onomastus* by the massive palpal conductor (Fig. 4B, E, F) and its geographical distribution.

FEMALE. Unknown.

MALE HOLOTYPE. *Carapace* (Fig. 4A, C): pale yellow grading to whitish yellow in eye region; fovea very indistinct. *Eyes*: with black surrounds except AM; fringed in shining white hairs. *Clypeus*: clothed in shining white hairs. *Chelicerae*: small, strongly inclined posteriorly; pale yellow, shiny; teeth not examined. *Maxillae and labium*: inclined posteriorly; pale yellow. *Sternum*: pale yellow. *Abdomen*: whitish yellow with scattered light brown hairs; spinnerets pale yellow-brown. *Legs*: pale yellow, tinged iridescent green; spines strong and numerous especially on legs I-II. Spination of legs I: metatarsi V 2–2–0, P 1–0–1, R 1–0–1; tibiae V 4–4–2, R 0–0–1, D 1–0–1; patellae R 0–1–0; femora P 0–0–1, D 1–1–1, R 0–0–1. *Palp* (fig. 4B, D, E, F): embolus (e) exceedingly long and thread-like; conductor (c) with massive lobe (t) and well developed embolic guide (eg); median apophysis (ma) with distal translucent flange; tegular apophysis (y) obscured by tibiae and patellae (easily overlooked).

Dimensions (mm): total length about 3·1; carapace length 1·4, breadth 1·18, height 0·6; abdomen length 1·6; eyes, AM row 0·74, AL row 1·08, PM row 0·68, PL row 0·70; quadrangle length 0·64. *Ratios*: AM : AL : PM : PL : 9·2 : 6 : 1 : 5; AL—PM—PL : 4 : 5; AM : CL 9·2 : 3.

DISTRIBUTION. Borneo.

MATERIAL EXAMINED. Holotype ♂, Indonesia: Borneo, Santan, Kalimantan, 3.vii.1976 (*R. Thomson*) (BMNH. 1979.7.4.1).

REMARKS. The indentation on the lower margin of the carapace (Fig. 5C) and the posteriorly inclined chelicerae, maxillae and labium provide additional space for the massive palps. From their inclination and size, the chelicerae appear rather ineffectual, suggesting that males do not feed after reaching maturity.

Acknowledgement

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The genus *Atropacarus* Ewing (Acari: Cryptostigmata)

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Introduction

The genus *Atropacarus* (type, *Hoplophora stricula* C. L. Koch) was proposed by Ewing (1917) for monodactyl 'Hoplodermatinae' (= Euptyctima) with a sculptured integument but without a median aspal carina. Jacot later (1930) submerged the genus in *Steganacarus*, giving it subgeneric ranking with *Tropacarus*, while Grandjean (1934) regarded the presence of an additional pair of setae in the posterolateral region of the notogaster as sufficient reason for retaining *Atropacarus* as a separate genus. Although *Atropacarus* has remained monotypic, Sheals (1969), in the course of a numerical taxonomic study of certain Phthiracaroidea, recognized three further species which he considered might be classified in this genus. These were *Steganacarus diaphanum* Jacot and two undescribed *Steganacarus* species from Italy and Nepal; the latter is here regarded as a 'variant' of *S. striculus* and the former as *Steganacarus clavigerus* (Berlese). Together with *striculus*, these species formed a distinct component within *Steganacarus* in being relatively small (notogastral length 300–475 µm), possessing at least 16 pairs of notogastral setae and having a coupled solenidion on tibia IV (this solenidion is free throughout the rest of the genus). However, while size is usually given in modern descriptions, there is little information available on the chaetotactic pattern of the legs and notogaster, but it would seem that the combination of characters exhibited by the above species may be present in further described species of *Steganacarus*. Accordingly, a search was undertaken of all the available *Steganacarus* material which superficially resembled *striculus*—the results of a preliminary survey indicated that the genus *Atropacarus** should be retained.

Genus *ATROPACARUS* Ewing

Atropacarus Ewing, 1917 : 131; Balogh, 1972 : 43.
Steganacarus: Jacot, 1930 : 210 (in part).

DEFINITION: Moderately sclerotized, rather elongate Phthiracaridae ranging in length from about 300–500 µm (lateral measurement of notogaster taken from the anterodorsal limit of the collar to a point just ventral to seta h_1). The integument of the dorsal and ventral shields is usually strongly ornamented while that of the infracapitulum, chelicerae and appendages is densely punctate. The interlamellar and lamellar setae are short and procumbent and the aspis bears a median keel. Sensillus cranked near the base. The notogaster bears at least 16 pairs of setae. A notogastral cowl may be present or absent. Fissures *ip* and *ips* are absent. Four pairs of anal setae are located on the paraxial margins of the anal plates and a single pair of adanals submarginally. There are at least seven pairs of genital setae along the paraxial margins of the genital plates. On tarsus I the posterior anterolateral seta is reduced and inserted adjacent to, or distally, in relation to the posterior fastigial seta. On leg IV the tibial solenidion is coupled.

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*Since this manuscript went to press a paper has been published by Aoki (25 March, 1980. *Bull. Inst. Sci. Technol. Yokohama* **6**(2): 1–88.) in which he separates *Atropacarus* from *Steganacarus* to include the species *A. phyllophorus*, *A. serratus* and *A. striculus*. Therefore, in the present paper *Atropacarus phyllophorus* is not a new combination.

Bull. Br. Mus. nat. Hist. (Zool.) **39** (3) : 189–204 Issued 27 November 1980

DIAGNOSIS: *Atropacarus* can be distinguished as a phthiracarid genus with the following combination of characters:

1 Notogaster with 16 or more pairs of setae.
2 Posterior anterolateral seta on tarsus I reduced.
3 Solenidion on tibia IV coupled with a reduced dorsal seta.

Key to species of the genus *Atropacarus*

1 Notogaster with 20 pairs of broad, serrated setae (Fig. 13); setae (*il*) and (*la*) more or less equal in length (Fig. 16); seta *a''* about half as long as famulus and closely associated with seta *ft''* (Fig. 19) . . . . ***A. clavigerus*** (Berlese) (p. 195)

– Notogaster with 16 pairs of setae (Fig. 4); setae (*il*) at least twice the length of (*la*) (Fig. 2); seta *a''* almost as long as famulus and located on a level with solenidion ω_2 (Fig. 9) . . 2

2 Notogaster without a cowl (Fig. 4); setae stout and serrated distally (Fig. 33) . . ***A. striculus*** (C. L. Koch) (p. 190)

– Notogaster with a well-developed cowl (Fig. 20); setae not of this form 3

3 Notogastral setae spatulate and serrated (Fig. 20); integument reticulate . . . ***A. phyllophorus*** (Berlese) (p. 197)

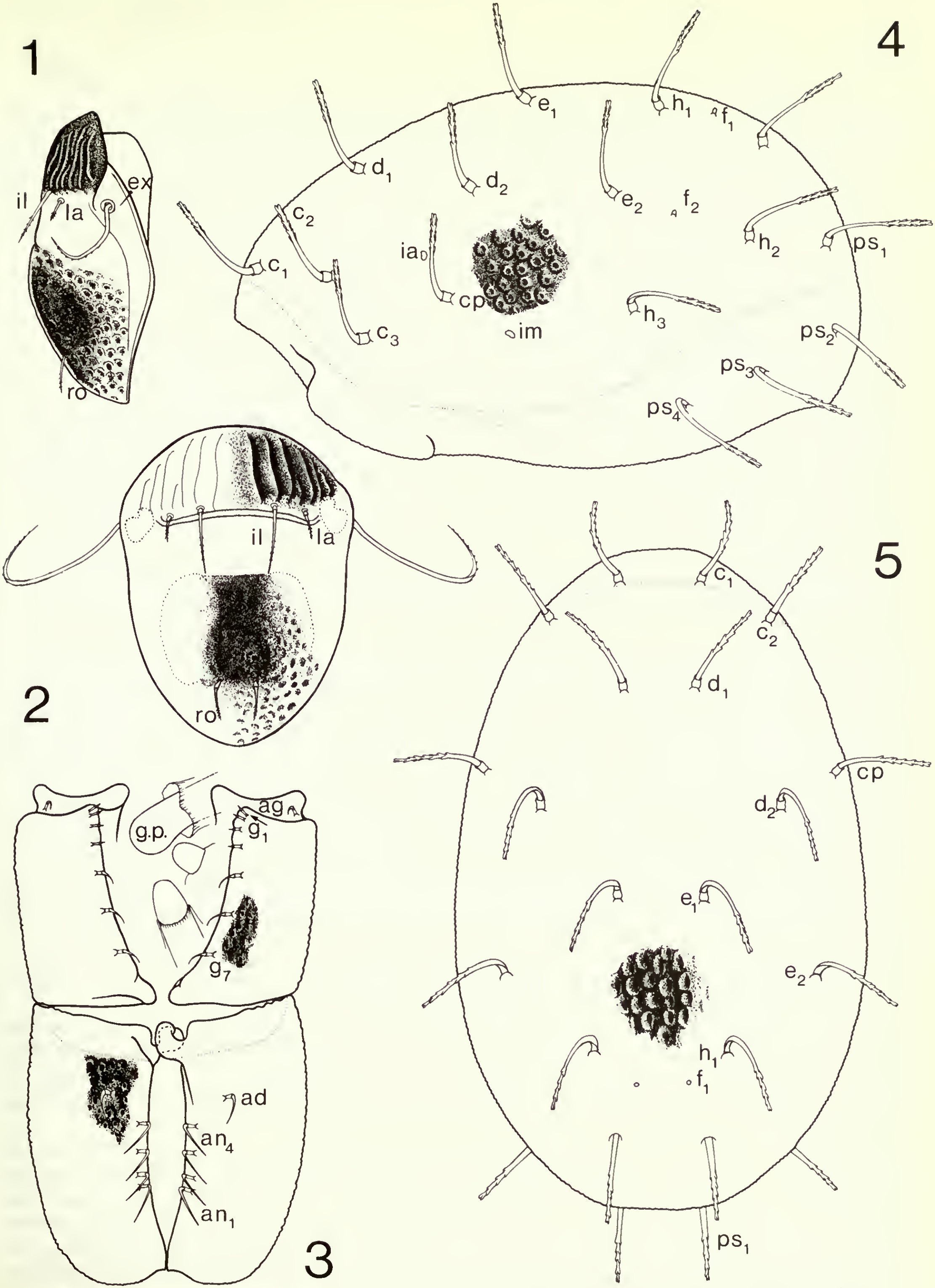
– Notogastral setae stout and apparently smooth (Fig. 27); integument rugose . . ***A. terrapene*** (Jacot) (p. 200)

Atropacarus striculus (C. L. Koch)
(Figs 1–12; 27–32)

Hoplophora stricula Koch, 1836 : Fasc. 2 t.10. [Type series lost.] NEOTYPE (here designated) (ZM, Hamburg , reg. no. A91/79). [See under 'Material' below.]
Atropacarus striculus: Ewing, 1917 : 131; Balogh, 1972 : 137.
Steganacarus diaphanum Jacot, 1930 : 236. 'Cotypes', Monroe, Connecticut (MCZ, Cambridge, Mass., no. 261hl). [Examined.] **Syn. nov.**
Hoploderma striculum: Willmann, 1931 : 190.
Steganacarus striculum: Grandjean, 1933 : 314.
Steganacarus striculus: Jacot, 1936 : 183; Feider & Suciu, 1957 : 33; Aoki, 1958 : 174; Sellnick, 1960 : 128. [Pérez-Iñigo, 1972 : 190. Misidentification.]
Stegenacarus senex Aoki, 1958 : 172. Holotype, Utsukushigahara (NUY, Tokyo). [Synonymized by Fujikawa, 1972 : 132.]
Steganacarus striculus insularis Weigmann, 1976 : 6. Holotype only, Azores (ITAZ, Berlin). [Examined.] **Syn. nov.** [1976 : 7 (Material from Teneriffe described by Pérez-Iñigo, 1972 : 190). Misidentification.]

Aspis (Figs 1–2; 28): 180–230 µm long and with a greatest width of 141–163 µm. All the dorsal setae are moderately short, procumbent and serrated distally. The lamellar (*la*) and interlamellar setae (*il*) are located at the level of the bothridia. Setae (*il*) are at least twice the length of setae (*la*) and extend about one-third of the distance between the bases of setae (*il*) and (*ro*). The sensillus, 86–114 µm in length (but see *striculus insularis* below), is slender, smooth and cranked near the base (Fig. 28); distally the sensillus is serrated and tapers to a fine point. Three finger-like tracheoles are associated with each bothridium and there is a single pair of short exobothridial setae (*ex*). There is a rather low, broad, median keel in front of the *il-la* setae while posteriorly the integument is raised into a number of longitudinal ridges. The prodorsal integument is opalescent and distinctly pitted.

Notogaster (Figs 4–5; 27; 29–30): 375–475 µm in length and with a greatest depth of 225–300 µm. The notogaster carries 16 pairs of setae, all of which are stout, erect, serrated distally (Fig. 30) and shorter than the distance c_1–d_1. Setae c_1 and c_3 are inserted close to the posterior margin of the collar and seta c_2 submarginally. In comparison with species of the genus *Steganacarus*, *A. striculus* has an additional pair of setae in the posterior region of the notogaster between setae h_1 and ps_1. The vestiges of setae f_1 and f_2 are present, f_1 being located just posterior to seta h_1, and f_2 between e_2 and h_2. The fissures *ip* and *ips* are absent. The integument is opalescent and generally distinctly pitted (Fig. 29).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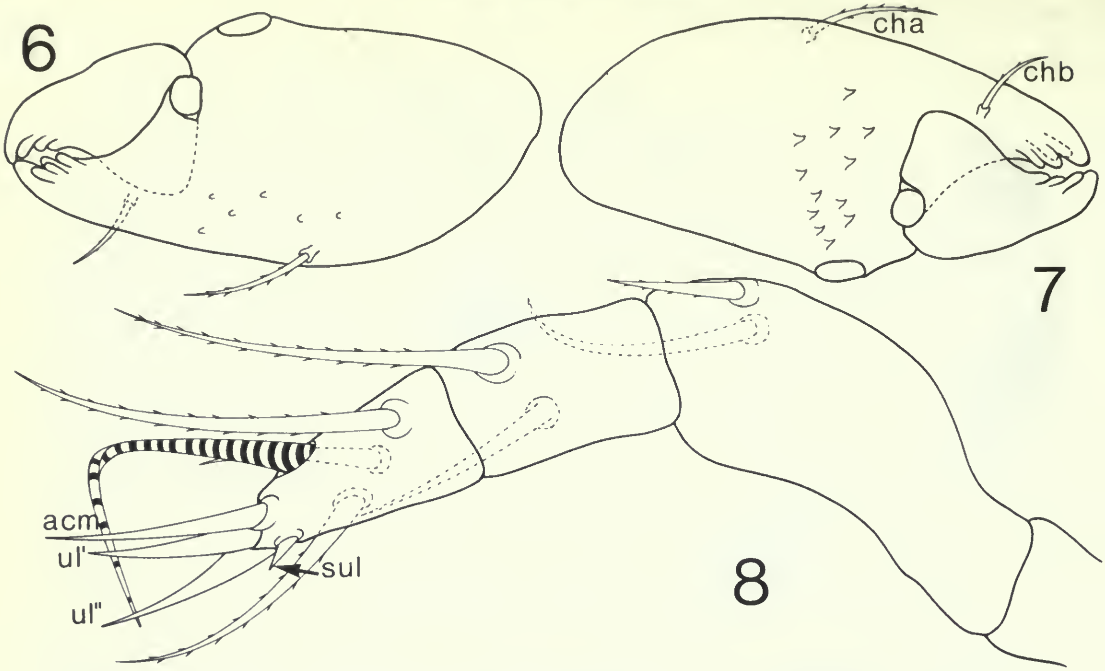
Figs 1–5 *Atropacarus striculus*: (1) aspis, lateral; (2) aspis, dorsal; (3) ano-genital region; (4) notogaster, lateral; (5) notogaster, dorsal.



Figs 6–8 *Atropacarus striculus*: (6) chelicera, antiaxial; (7) chelicera, paraxial; (8) pedipalp.

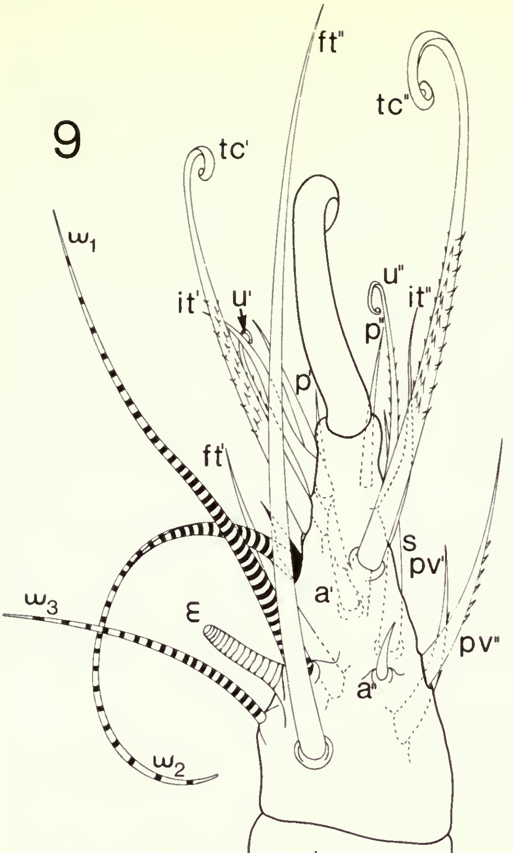
Ano-genital region (Figs 3; 27): On each anal plate there are four pairs of marginal anal setae (an_{1-4}) and a single pair of adanals (*ad*) located submarginally and rather far forward. Setae an_{1-4} are more or less equal in length and about twice as long as the adanal setae. Ventrally, each anal plate has a prominent anteromedian lobe, the left overlying the right ('right-fitting' arrangement, see van der Hammen, 1963). There are usually seven pairs of genital setae (g_{1-7}) arranged in a pattern 4 + 3 along the paraxial margins of the genital plates, setae g_{1-4} being approximately half the length of setae g_{5-7}. A single aggenital seta *ag* is located antiaxially in the genital furrow. The integument of the ano-genital region is distinctly pitted with the exception of the setae-bearing areas which have no ornamentation. There are three pairs of genital papillae ($g.p._{1-3}$), the anterior pair ($g.p._1$) being rather small.

Infracapitulum: Typically phthiracaroid in form (see, for example, Parry, 1979). There are three pairs of adoral setae, the anterior pair being brush-like distally and the posterior two pairs weakly serrated.

Pedipalps (Fig. 8): Three-segmented with the setal formula (2–2–7). Four of the tarsal setae (*acm*, *ul′*, *ul″* and *sul*) are eupathidial, *sul* being the shortest.

Chelicerae (Figs 6–7): The movable digit has three distinct teeth and the fixed digit carries five. The latter are arranged in two rows, an inner one of three teeth and an outer one of two. The principal segment carries about six conical spines on the antiaxial surface and about 12 sharply pointed spines paraxially. Setae *cha* and *chb* are both serrated, *cha* being somewhat longer than *chb*.

Legs (Figs 9–12; 31–32): The solenidial formulae for the legs are I (2–1–3); II (1–1–2); III (0–1–1) and IV (0–1–0). All the solenidia are rather long, usually with a single coil distally. Solenidion ω_2 on tarsus I is coupled with a small distal seta (Fig. 31). The latter was first observed in *S. striculus* by Griffiths and Sheals (1971) who described the seta as being sabre-shaped. On all legs the tibial solenidion Φ is coupled with a reduced dorsal seta (Fig. 32) while on genu I solenidion σ_1 is coupled with a reduced posterolateral seta (l''). The formulae for the leg setae are I (1–4–2–5–16–1); II (1–3–2–3–12–1); III (2–2–1–2–10–1) and IV (2–1–1–2–10–1). On tarsus I six of the setae (*s*, (*it*), (*p*) and *a′*) are eupathidial. The famulus ε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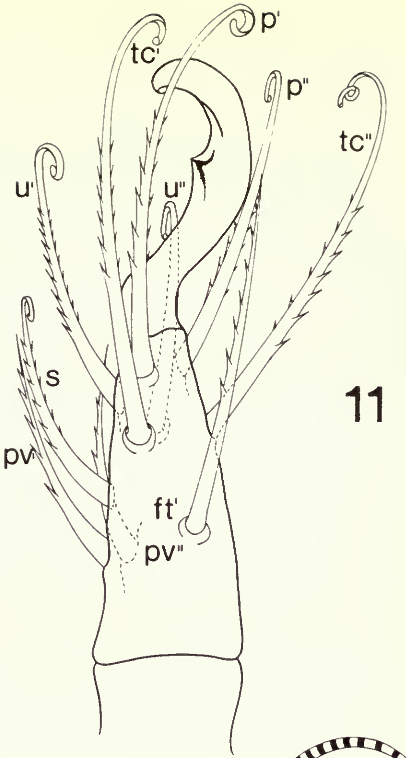
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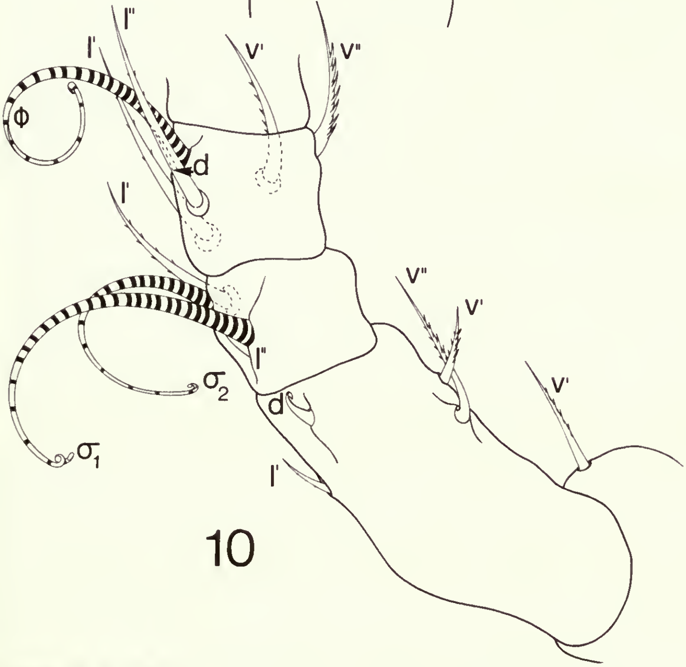
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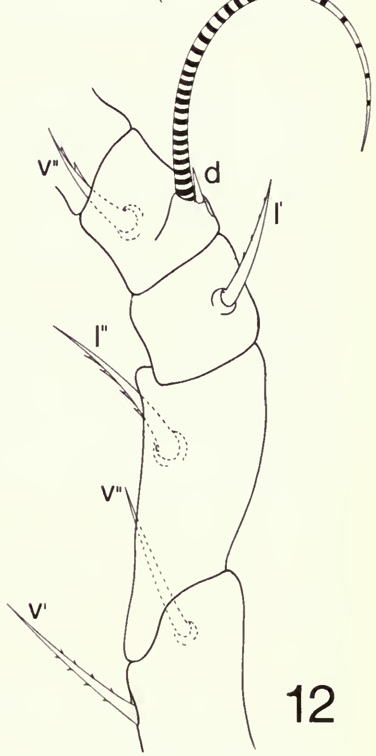


Figs 9 & 10 *Atropacarus striculus*, posterolateral aspect of leg I: (9) tarsus; (10) tibia to trochanter.

Figs 11 & 12 *Atropacarus striculus*, anterolateral aspect of leg IV: (11) tarsus; (12) tibia to trochanter.

(Figs 9 and 11 are drawn at the same magnification.)

is rugose and closely associated with ω_1. Seta *a''* is short (approximately half as long as the famulus), smooth and located on a level with the solenidion ω_1. Setae (*tc*) and (*u*) on tarsus I and (*tc*), (*u*), (*p*) and *s* on tarsi II to IV are ribbon-like, hooked distally and covered with whorls of spicules in the middle third. Seta *d* on femur I is rather short, hooked distally and apparently smooth, while the anteroventral seta *v'* on this segment is comparatively short and stout. On all segments the ventral setae (*v*) bear two or three rows of distinct serrations while the lateral setae (*l*) carry only a few weakly-developed serrations. All the tarsi terminate in a single claw bearing two ventral teeth.

MATERIAL: Material was examined from the following unnamed and unsorted collections of the British Museum (Natural History): beech litter, Box Hill, Surrey, August, 1973 (K. H. Hyatt); beech litter, Chalfont St. Giles, Buckinghamshire, 8.xi.64 (J. G. Sheals); hedgerow litter, Peterborough, Cambridge, 23.i.78 (P. N. Lawrence & B. R. Pitkin); *Sphagnum* litter, Hartland Moor, Dorset, 8.xi.63 (P. N. & K. Lawrence); yew humus, Manor Wood, Rothamsted Experimental Station, Hertfordshire, 22.viii.61 (P. N. Lawrence); deciduous humus, Roudsea Woods, Grange-over-Sands, Lancashire, 24.ix.62 (P. N. Lawrence); alder litter, Westwood Marshes, Suffolk, 8.iii.64 (P. N. & K. Lawrence); mixed hawthorn and sallow litter, Woodwalton Fen, Huntingdonshire, 18.ix.63 (P. N. & K. Lawrence); soil in cracked rock, Inchiquin Lough, Co. Clare, 9.vii.60 (P. N. Lawrence); sycamore humus, Newtown Castle, Co. Clare, 5.vii.60 (P. N. Lawrence); rhododendron humus, Milke Danre, East Nepal, 2.xii.61 (J. G. Sheals); forest litter, Kronåsen, Sweden, 23.v.64 (P. N. Lawrence). Material was also examined from: moss on branches of *Juniperus brevifolia*, Faial, Azores, 19.vi.69 (P. Ohm) (ITAZ, Berlin); moss, Donaustaufer Forest, Regensburg, West Germany, 14.viii.59 (M. Sellnick) (ZM, Hamburg) (one of these specimens, now dissected and mounted in Berlese's fluid, is hereby designated as the *neotype*); litter and humus under *Fagus crenata*, Kuromatsunai, Japan, 25.xi.68 (T. Fujikawa) (NSM, Tokyo).

REMARKS: *Hoplophora stricula* was described by Koch from marshy places near Regensburg, West Germany. Although Koch's original specimens are presumed to be lost, his figures and description permit reidentification.

Material collected at Regensburg by Dr Max Sellnick has been compared with specimens from the British Isles, Japan and Nepal. With the exception of the British material, the general form of the aspis and notogaster and their setal arrangements appear to be identical. However, amongst the British population, a number of 'variants' were observed in which femur I carried four setae and genu IV carried no setae. Moreover, the 'femur I–4, genu IV–0' condition (see also, Parry, 1979) was invariably associated with the presence of one or two additional pairs of setae on the genital plates (total 8 or 9 pairs respectively) while on the notogaster the setae were always rather short and weakly serrated. By contrast, the notogastral setae of the Nepalese specimens (see also, Sheals, 1965) were very much stouter and more strongly serrated than those of the other populations. Again, amongst the British 'variants', the aspal carina was only weakly developed while the lamellar setae were considerably less than half the length of the interlamellars. The sensilli appear to be identical in all four populations.

The single specimen of *striculus insularis* collected on the Azores has also been compared with the Regensburg material and the following differences noted: aspal crest somewhat lower than in typical *A. striculus*; lamellar setae considerably shorter than half the interlamellar length; sensilli about 65 µm long and slightly thickened; notogastral setae relatively shorter and more slender than in typical *A. striculus*; notogastral integument punctate as in species of the genus *Phthiracarus*; nine pairs of genital setae (Weigmann figures only eight pairs) arranged in a pattern of 5 + 4 along the paraxial margins of the genital plates; genu IV–0. Bearing in mind the degree of variation observed in the populations studied above, it seems inadvisable at the present time to warrant the single specimen from the Azores with subspecific ranking.

Steganacarus spinosus, recorded by Sellnick (1920) from humus in the woods around Lötzen, West Germany, closely resembles *A. striculus*, and it seems likely that in the past the identities of these two species have been confused. Two specimens, determined by Sellnick from Patscherkofel, Nordtirol, Austria have been examined and although they have been found to fall within the size range given above for *striculus* (notogastral length 375–475 μm), the notogaster bears only 15 pairs of setae while the solenidion on tibia IV is free.

Atropacarus clavigerus (Berlese) comb. nov.
(Figs 13–19)

Hoploderma clavigerum Berlese, 1904 : 275; 1913 : 104. Holotype, Pisa, Italy (ISZA, Florence, no. 141/9). [Photographs examined.] [Schweizer, 1956 : 363. Misidentification.]
Hoploderma clavigera: Sellnick, 1929 : 40.

Aspis (Figs 16–17): 188–246 μm long and with a maximum width of 127–165 μm. All the dorsal setae are short, stout and distinctly feathered. Setae (*il*) and (*la*) are more or less equal in length and extend to the anterior limits of the bothridia. The sensilli, 77–96 μm in length, are expanded and serrated distally, while the basal portion is smooth, slender and distinctly cranked. In front of the *il-la* setae there is a prominent median keel and posteriorly the integument is raised into a number of longitudinal and transverse ridges. The ornamentation of the prodorsal integument (apparently always encrusted with detritus) is rather striking and may be described as raised reticulate.

Notogaster (Figs 13–14): The notogaster ranges in length from 354–467 μm with a greatest depth of 188–283 μm. There are 20 pairs of setae, all of which are very short (less than c_1-d_1), stout and bear three or four whorls of blunt serrations. In comparison with the notogastral chaetotaxy of *striculus*, *A. clavigerus* has four additional pairs of setae, one in the *c* series, another in the *h* series, and two pairs in the *ps* series. The vestiges of setae f_1 and f_2 are present, f_1 being located ventral to the seta h_1, and f_2 ventral to the seta e_2. The notogastral integument is ornamented in a raised reticulate pattern.

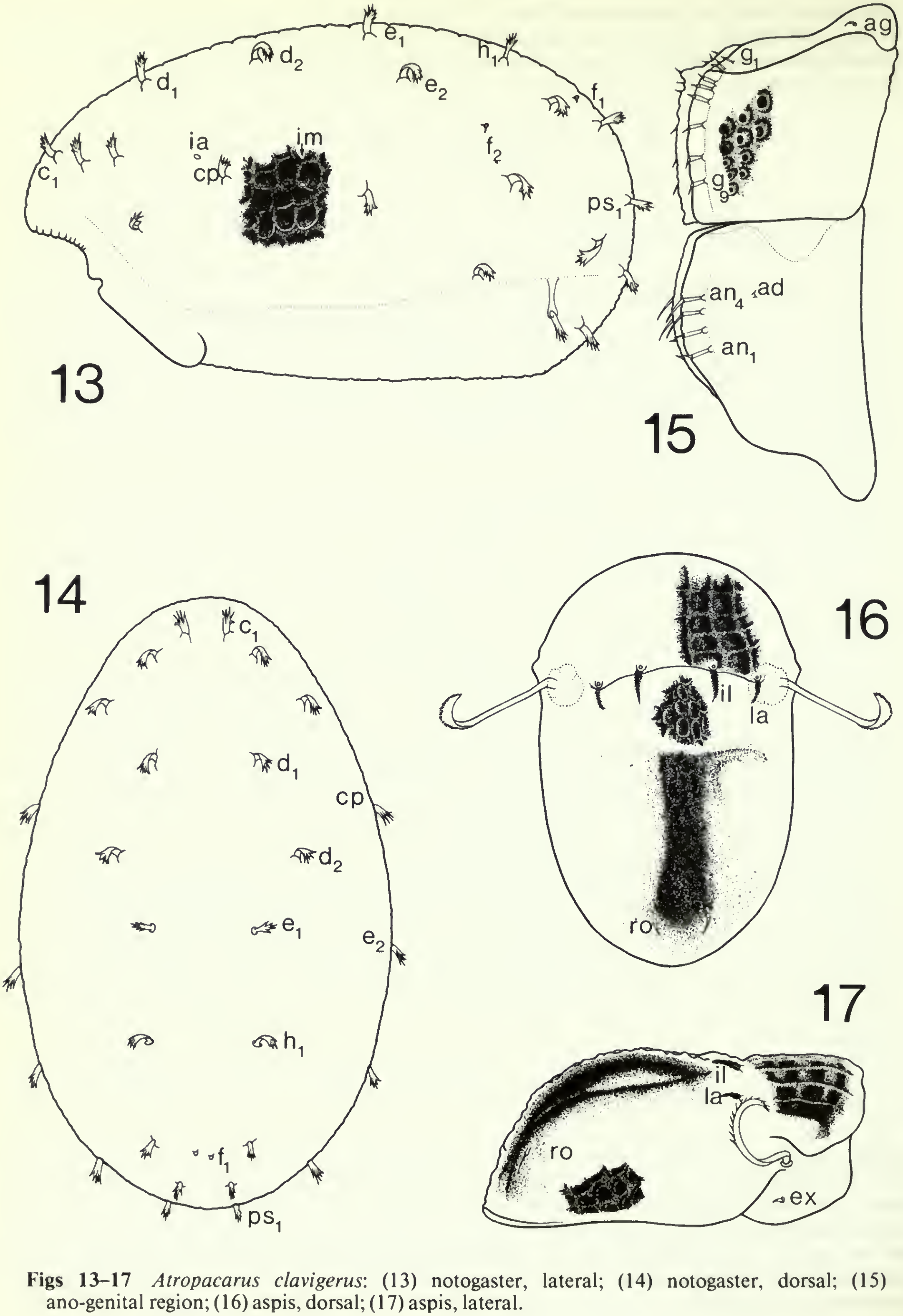
Ano-genital region (Fig. 15): The four pairs of anal setae (an_{1-4}) are located marginally with a single pair of adanals (*ad*) (missing in specimen figured) located submarginally and rather close to (an_4). All the anal setae are short, the anterior two pairs (an_{3-4}) being approximately twice as long as the posterior two. There are nine pairs of minute genital setae (g_{1-9}) arranged in a pattern of 6 + 3 along the paraxial margins of the genital plates. The ornamentation of the genital and anal plates is similar to that of the notogaster.

Chelicerae: The chelicerae resemble those of *A. striculus* although the antiaxial and paraxial surfaces carry a smaller number of spines.

Legs (Figs 18–19): The setal and solenidial formulae for the legs are as in *A. striculus*. All the solenidia are long and straight. On tarsus I the seta coupled with solenidion ω_2 is short with only a weakly developed distal process (see Parry, 1979). Seta *a″* is rather short (approximately half as long as the famulus) and closely associated with the long posterior fastigial seta *ft″*. Setae (*tc*) and (*u*) on tarsus I and (*tc*), (*u*), (*p*) and *s* on tarsi II to IV are ribbon-like, hooked distally and bear whorls of sharply pointed spicules in the middle third. On femur I seta *d* is short and somewhat thickened while seta *v′* on this segment is stout and strongly serrated.

MATERIAL: Eight specimens, BMNH 1979.6.21.6–13, from oak litter (*Quercus ilex*), Boboli Gardens, Florence, Italy. The material was collected by Dr J. G. Sheals, 18 March 1971.

REMARKS: Berlese (1904) recorded *clavigerus* from dead leaves in the Boboli Gardens, Florence, but described the type of the species from Pisa. Unfortunately, we have not been able to examine the holotype but we have studied photographs of the latter taken by Dr J. G. Sheals (BMNH). The specimen appears to be in good condition and although undissected the integumental ornamentation and chaetotactic characters can be discerned. Material collected from the Boboli Gardens has been compared with photographs of the holotype—no morphological differences could be detected.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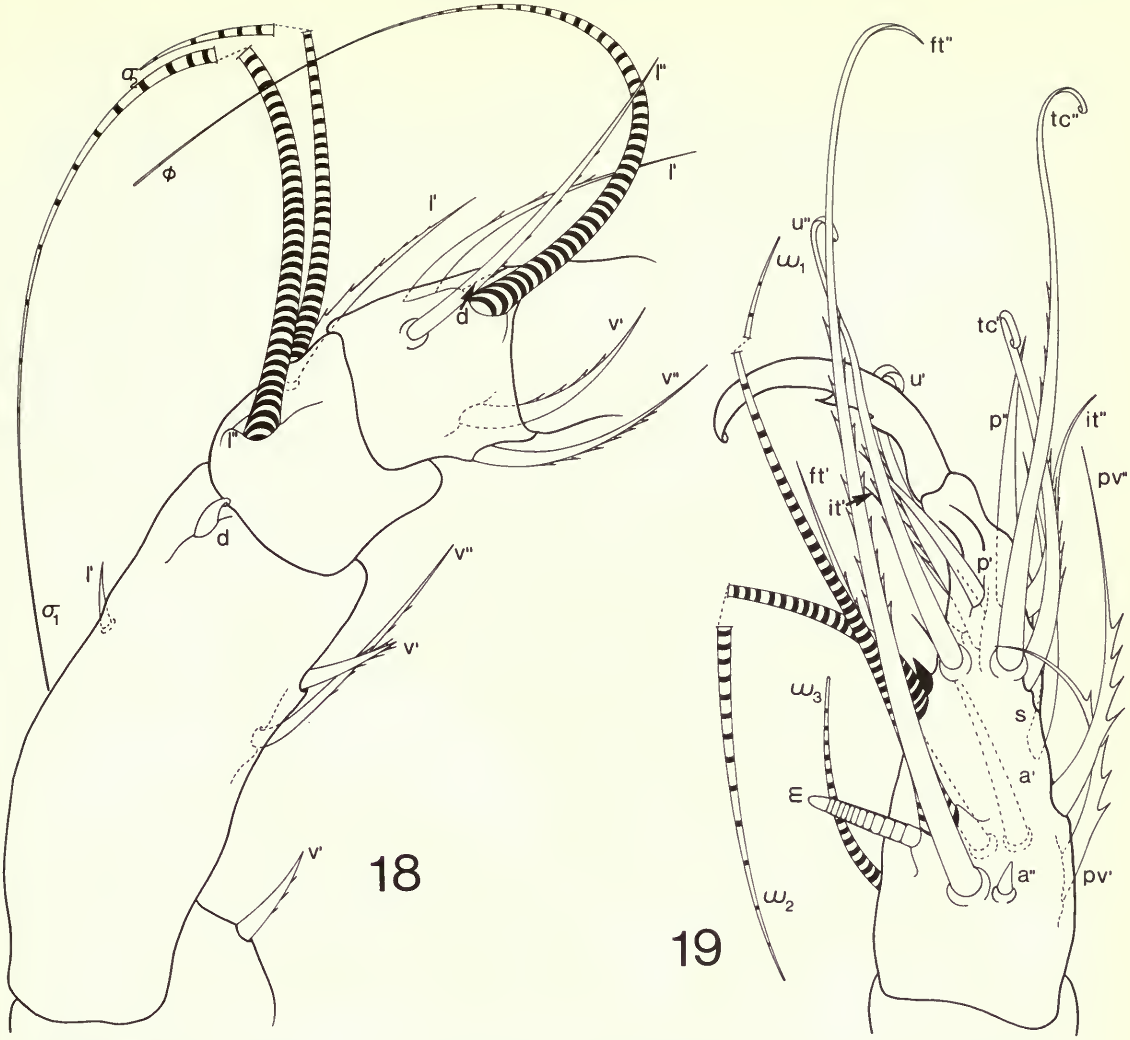
Figs 13–17 *Atropacarus clavigerus*: (13) notogaster, lateral; (14) notogaster, dorsal; (15) ano-genital region; (16) aspis, dorsal; (17) aspis, lateral.



Figs 18 & 19 *Atropacarus clavigerus*, posterolateral aspect of leg I: (18) tibia to trochanter; (19) tarsus.

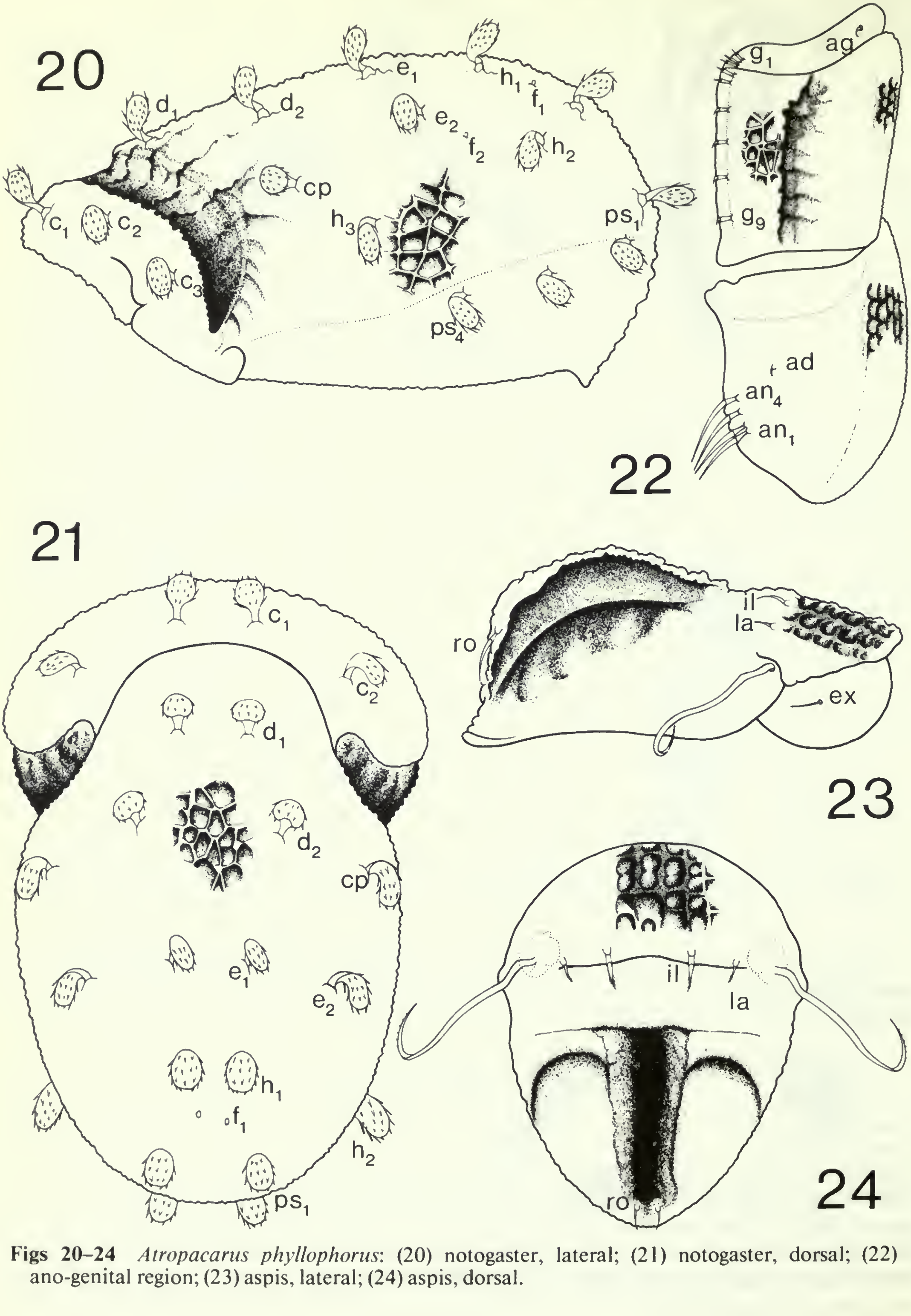
A. clavigerus differs from the other members of the genus by having four additional pairs of setae on the notogaster. Moreover, the very striking ornamentation of the prodorsal and notogastral integument serves to characterize this species.

Atropacarus phyllophorus (Berlese) comb. nov.*
(Figs 20–26)

Hoploderma phyllophorum Berlese, 1904 : 275; 1913 : 103. Holotype, Florence, Italy (ISZA, Florence, no. 57/46).
Steganacarus phyllophorus: Schuster, 1957 : 97; 1965 : 218.
Steganacarus ropalus Feider & Suciu, 1957 : 35. [Synonymized by Schuster, 1965 : 218.]

Aspis (Figs 23–24): 196–208 μm long and with a greatest width of 138–145 μm. All the dorsal setae are short, stout and brush-like distally. Setae (*il*) are about twice the length of setae (*la*) and together form a transverse row behind which the prodorsal integument is raised

*See footnote at bottom of p. 189.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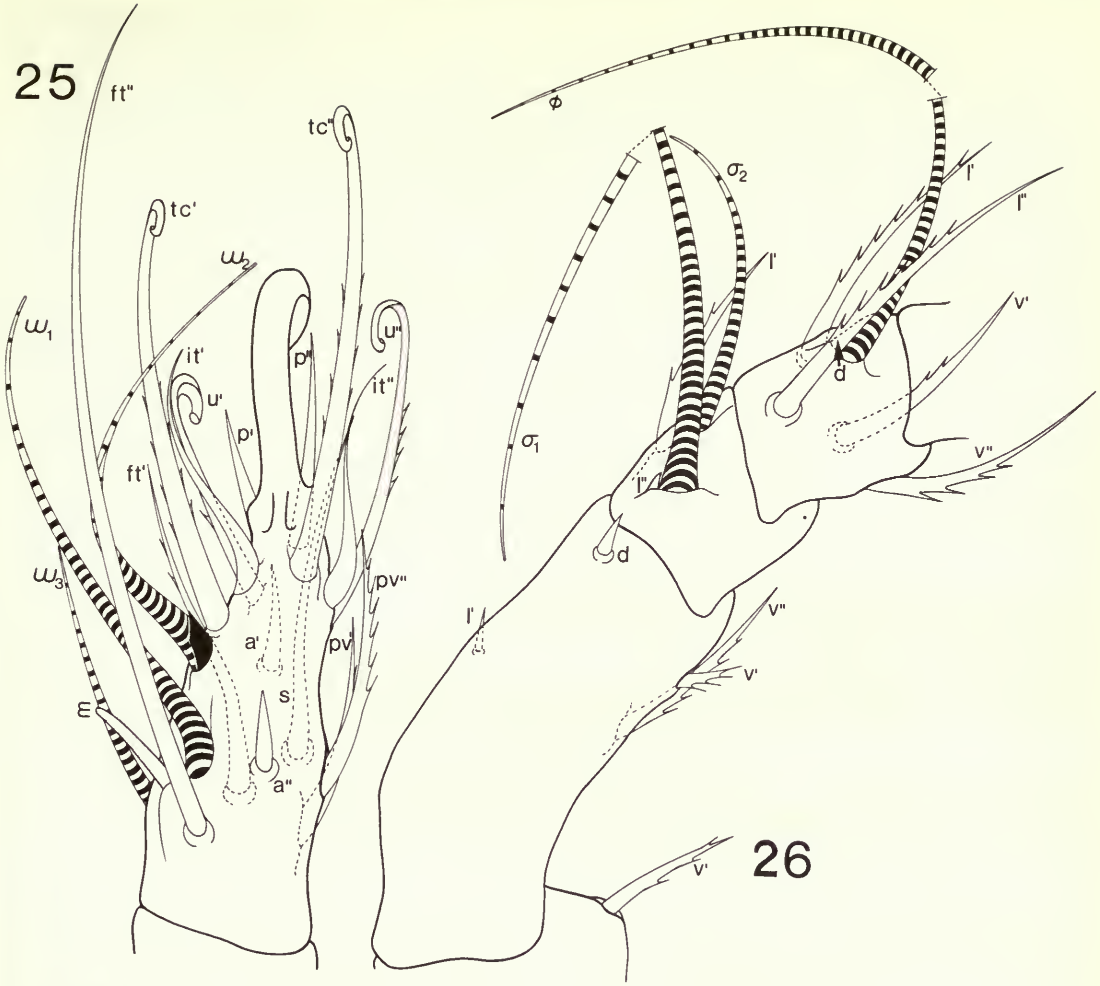
Figs 20–24 *Atropacarus phyllophorus*: (20) notogaster, lateral; (21) notogaster, dorsal; (22) ano-genital region; (23) aspis, lateral; (24) aspis, dorsal.



Figs 25 & 26 *Atropacarus phyllophorus*, posterolateral aspect of leg I: (25) tarsus; (26) tibia to trochanter.

into a number of irregularly arranged longitudinal and transverse ridges. The sensillus is 97–111 μm in length and closely resembles that of *A. striculus*. In front of the *il-la* row there is a broad and rather pronounced median keel. The integument is sculptured in a reticulate pattern.

Notogaster (Figs 20–21): 376–446 μm in length and with a greatest depth of 198–238 μm. The notogastral chaetotaxy closely resembles that of *A. striculus*. There are 16 pairs of setae all of which are rather short (less than c_1-d_1), broadly spatulate, and serrated marginally. Setae c_{1-3} form a row submarginally on the cowl, the latter being separated from the rest of the notogaster by a deep furrow which extends dorsolaterally. The vestiges of setae f_1 and f_2 are present. The integument is sculptured in a reticulate pattern.

Ano-genital region (Fig. 22): The four pairs of anal setae (an_{1-4}) are more or less equal in length and located marginally while a single pair of minute adanals (*ad*) are located submarginally and rather far forward. The integument of the anal plate is rugose. There are nine pairs of minute genital setae (g_{1-9}) arranged in a pattern of 5 + 4 along the paraxial margins of the genital plates. A median longitudinal ridge with irregular thickenings separates a reticulate paraxial region from a rugose antiaxial region.

Legs (Figs 25–26): The chaetotaxy and solenidiotaxy of the legs follows the typical *Atropacarus* pattern. All the solenidia are long and straight. On tarsus I the seta coupled with solenidion ω_2 is short and somewhat elongated distally. Seta *a″* is almost as long as the famulus and is located on a level with solenidion ω_1. Setae (*tc*) and (*u*) on tarsus I and (*tc*), (*u*), (*p*) and *s* on tarsi II to IV are ribbon-like, hooked distally and bear whorls of sharply pointed spicules in the middle third.

MATERIAL: We have examined material collected in 1956 by Dr R. Schuster who recorded this species from oak litter in Vienna, and from heathland and *Sesleria*-grassland in Weiz, Austria.

REMARKS: Although Berlese's (1904) original description of *phyllophorus* from specimens collected in rotting leaves, Boboli Gardens, Florence is extremely superficial, his figures (Berlese, 1913) show the characteristic features of the species: long sensillus serrated distally; spatulate notogastral setae; anterior cowl on notogaster; reticulate integument. Schuster's redescription of *phyllophorus*, based on material collected in Austria, is adequate although no information is available on the chaetotactic pattern of the legs.

The distribution of notogastral setae in *A. phyllophorus* is very similar to that shown for *A. striculus*. The additional seta is again located more or less mid-way between setae h_1 and ps_1 with vestigial f_1 located anterodorsally. The diagnostic features of *A. phyllophorus* are the notogastral cowl bearing setae c_{1-3} and the strongly spatulate notogastral setae.

Atropacarus terrapene (Jacot) comb. nov.
(Figs 27–29)

Steganacarus terrapene Jacot, 1937 : 165. 'Cotypes', Buncombe County, N. Carolina (MCZ, Cambridge, Mass., no. 35F6.2–36). [Examined.]

Aspis (Fig. 29): 164–208 μm in length. All the dorsal setae are short, stout and apparently simple. Setae (*il*) and (*ro*) are more or less equal in length and about twice as long as the lamellars (*la*). The sensilli are expanded and serrated distally, while the basal portion is smooth, slender and distinctly cranked. In front of the *il-la* row there is a pronounced and rather truncated median keel. The prodorsal integument is sculptured in a rugose pattern.

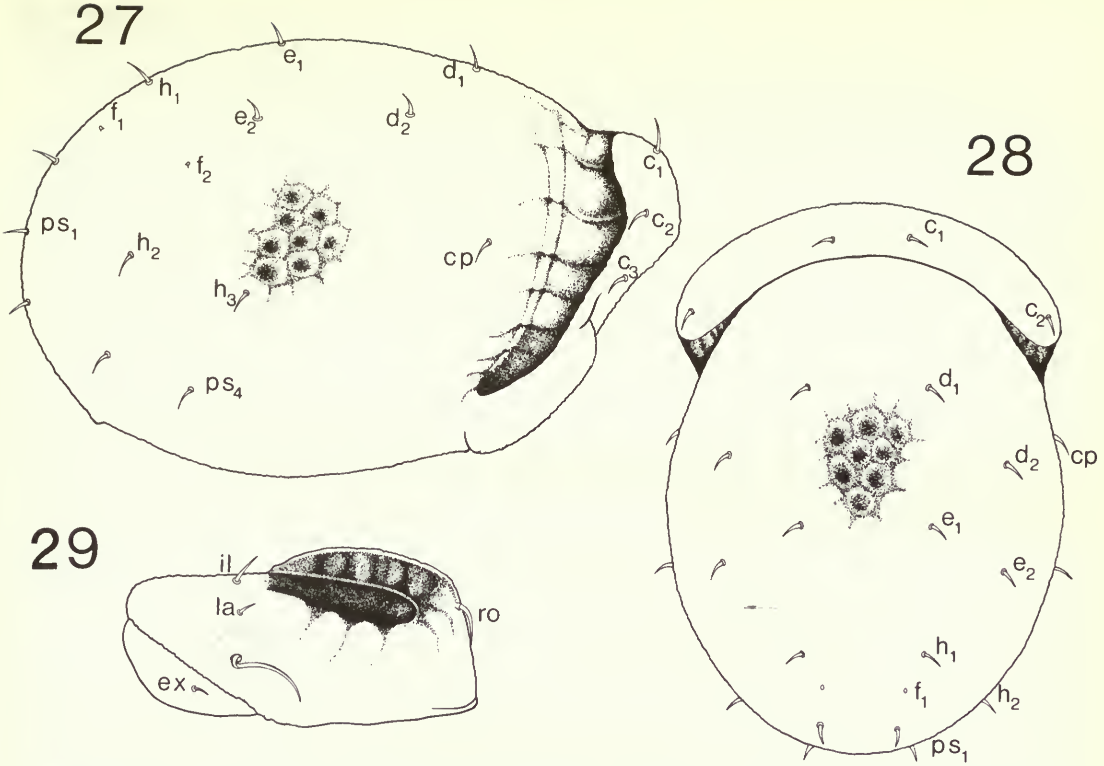
Notogaster (Figs 27–28): The notogaster ranges in length from 276–352 μm with a greatest depth of 184–240 μm. There are 16 pairs of setae all of which are very short (less than c_1-d_1), stout and apparently simple. Anteriorly there is a well defined cowl bearing setae c_{1-3}. The vestiges of setae f_1 and f_2 are present. The integument is rugose.

Ano-genital region: There are four pairs of marginal anal setae (an_{1-4}) and a single pair of adanals (*ad*) located submarginally and rather far forward. Setae an_{1-4} are more or less equal in length and distinctly longer than the adanals. On the genital plates the setal bases are difficult to discern owing to the rather opaque nature of the integument. However, there appear to be eight pairs of genital setae arranged in a pattern of 4 + 4 along the paraxial borders. The integument is rugose.

Legs: The setal and solenidial formulae for the legs are as in *A. striculus*. All the solenidia are long and straight. On tarsus I the seta coupled with solenidion ω_2 is very short. Seta *a″* is almost as long as the famulus and located on a level with solenidion ω_2. Setae (*tc*) and (*u*) on tarsus I and (*tc*), (*u*), (*p*) and *s* on tarsi II-IV are ribbon-like, hooked distally and bear whorls of sharply pointed spicules in the middle third.

MATERIAL: Eight 'cotypes' from oak litter, Bent Creek Experimental Forest, N. Carolina, U.S.A. The material was collected by Dr A. P. Jacot, 15 July 1935.

REMARKS: The eight 'cotypes' examined are in good condition and mounted in Canada Balsam. They are undissected and although only partially cleared, most of the chaetotactic characters can be discerned.



Figs 27–29 *Atropacarus terrapene*: (27) notogaster, lateral; (28) notogaster, dorsal; (29) aspis, lateral.

A. terrapene shows an overall similarity to *A. phyllophorus*. In both species the aspal keel is markedly truncated and the notogaster bears a well-developed cowl.

Survey

In addition to the species referred to above, a number of other taxa, possibly referable to *Atropacarus*, have been considered but unfortunately type material has not been available in the case of the following six species, all of which fall within the size range given for *Atropacarus*: *illinoisensis* (Ewing, 1909), *vitrinum*, *remigerus* and *somalicus* (Berlese, 1913, 1923 & 1923), *serratus* Feider and Suciu (1957), and *collaris* Balogh (1958).

In his original description of *Atropacarus*, Ewing (1917) noted that *illinoisensis*, of which the type specimen is apparently lost, was 'known to be included in the genus *Atropacarus*.' Although from the description and illustration the species does appear to have certain affinities with *Atropacarus* (sickle-shaped sensillus, stout pectinate notogastral setae, overall length 450 μm), the number and arrangement of setae on the anal plates (two marginal and three submarginal) are reminiscent of *Phthiracarus*. Moreover, the general shape of the aspis and the form of the integumental ornamentation are characteristic of a *Phthiracarus* species.

The true identities of the three species described by Berlese are doubtful, although it seems probable that they have been correctly assigned to the genus *Steganacarus*. Van der Hammen (1959) has examined each of the species which are entire, uncleared and mounted in Canada Balsam, and is of the opinion that they belong to a '*striculus*-group'. However, it seems unlikely that they can be reidentified in their present condition.

In their original description of *Steganacarus serratus*, a species recorded from mosses and leaves, Odorhei, Rumania, Feider and Suciu (1957) described the presence of 14 pairs of notogastral setae. However, it is apparent from their figure that *serratus* bears at least 16, or possibly even 19 pairs of setae on the notogaster. Unfortunately, there is no information available on the chaetotactic pattern of the legs but it is conceivable that the species may belong to the genus *Atropacarus*.

Steganacarus collaris, a species described from Angola(Balogh, 1958), cannot be determined as a member of the genus *Atropacarus* without a re-examination of the holotype for Balogh's description does not include details of any notogastral or leg chaetotactic characters.

The holotype of *Steganacarus craterifer*, collected by Hammer (1971) from dry leaves on Viti Levu, the Fiji Islands, has been examined. This species is of particular interest for it shares with all species of the genus *Atropacarus* the presence of a coupled solenidion on tibia IV while only possessing 15 pairs of setae on the notogaster (Hammer figures only 14 pairs). However, the general shape of the aspis and the form of the integumental ornamentation are reminiscent of species of the genus *Tropacarus*. The arrangement of setae on the genital and anal plates are nevertheless characteristic of *Steganacarus*.

Acknowledgements

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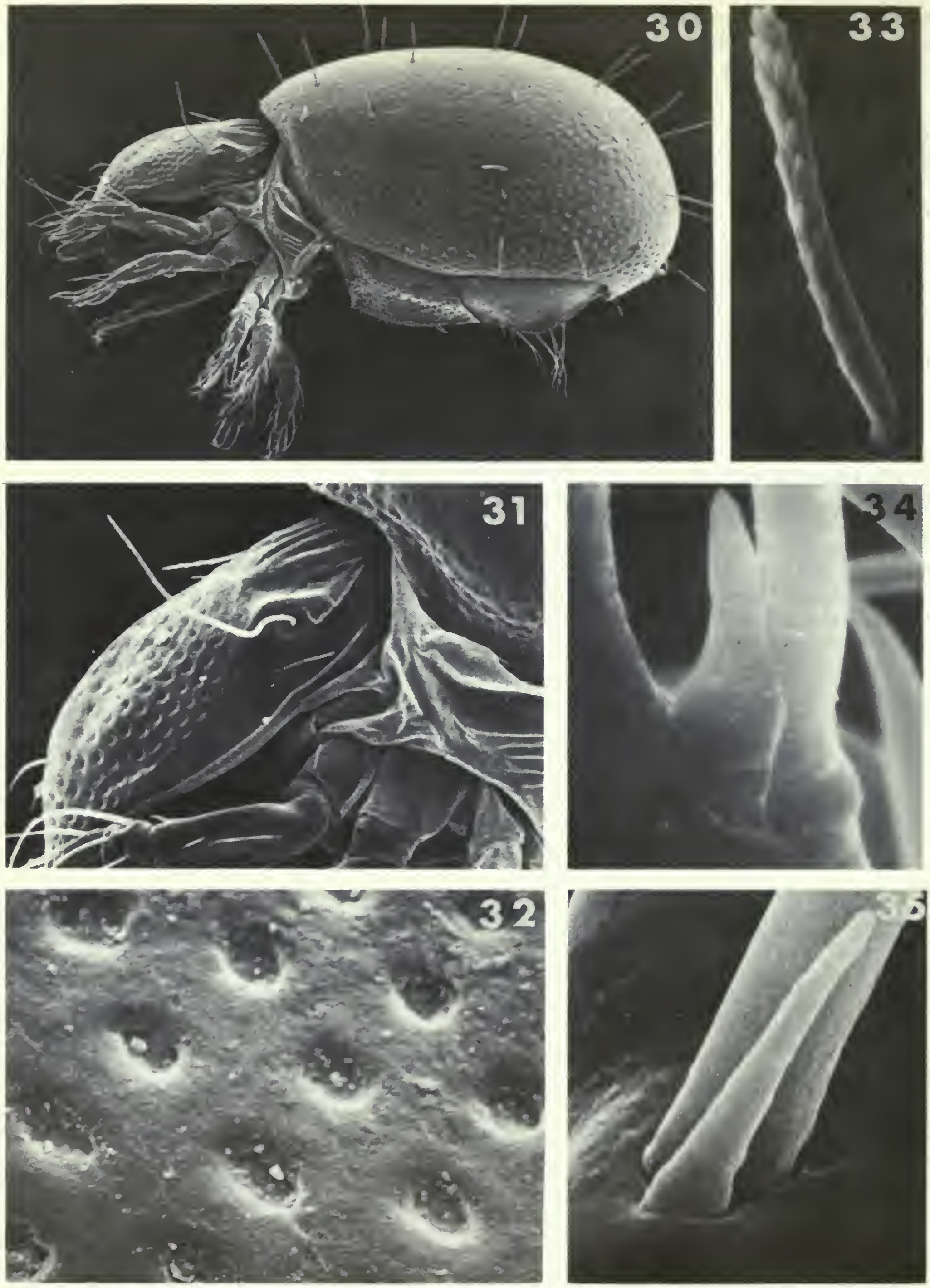

Figs 30–35 *Atropacarus striculus*: (30) lateral aspect, ×130; (31) aspis, lateral aspect, ×310; (32) detail of notogastral integument, ×4960; (33) detail of notogastral seta, ×1200; (34) distal solenidion and associated seta on tarsus I, anterolateral aspect, ×8440; (35) solenidion and associated seta on tibia IV, dorsal aspect, × 9110.

The first record of a rare murine rodent *Diomys* and further records of three shrew species from Nepal

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Synopsis

The rare genus *Diomys* is recorded from Nepal for the first time. Ecological notes and histograms displaying measurements of all the specimens in the apparently unique collection of this rodent in the British Museum (Natural History) are given. Also listed are museum specimens of *Crocidura attenuata*, *Sorex minutus* and *Suncus etruscus* which extend the known range of each of these species. Fleas collected from *Diomys crumpi* and *Crocidura attenuata* are also recorded.

Introduction

The study of material collected by the University of East Anglia Expedition to Nepal in 1978–1979 and the subsequent review of some of the collections from that country in the Mammal Section of the British Museum (Natural History) has shown the existence of specimens which extend the known ranges of three species of shrews, *Crocidura attenuata*, *Suncus etruscus* and *Sorex minutus* and a rare rodent *Diomys crumpi* last reported 33 years ago.

Diomys crumpi Thomas, 1917

Diomys crumpi Thomas, 1917 : 203. Holotype B.M.(N.H.) No. 15.4.3.146. Presumed type locality: Mt. Paresnath, Hazaribagh, Bihar, India, 4300 ft. [23°56′N 86°07′E].

The holotype, an incomplete skull which lacks the bullae, the posterior part of the braincase and m_3 on both sides was collected by Mr C. A. Crump, after whom it was named. It was mismatched with a skin of *Millardia meltada* collected on 13 June 1914 at the presumed type locality. For 29 years this was apparently the only recognized representative of the genus in any collection.

In February 1940 Wilfred J. C. Frost, collecting for Sir John Ellerman obtained a series of specimens from Bishenpur [24°40′N 93°45′E], Manipur, Assam at 3000 and 4000 ft. Although Ellerman had asked Frost to try to obtain some specimens of *Diomys* from Paresnath Hill, the supposed type locality, he was unable to do so because collecting was not allowed there (Ellerman, 1961 : 205).

In February 1946 additional specimens were obtained from Imphal [24°47′N 93°55′E] by Messrs J. Hake and T. J. Lawrence. These were registered in 1967 with material collected by the Scrub Typhus Research Team (see Roonwal, 1949) and do not appear to have been seen by Ellerman.

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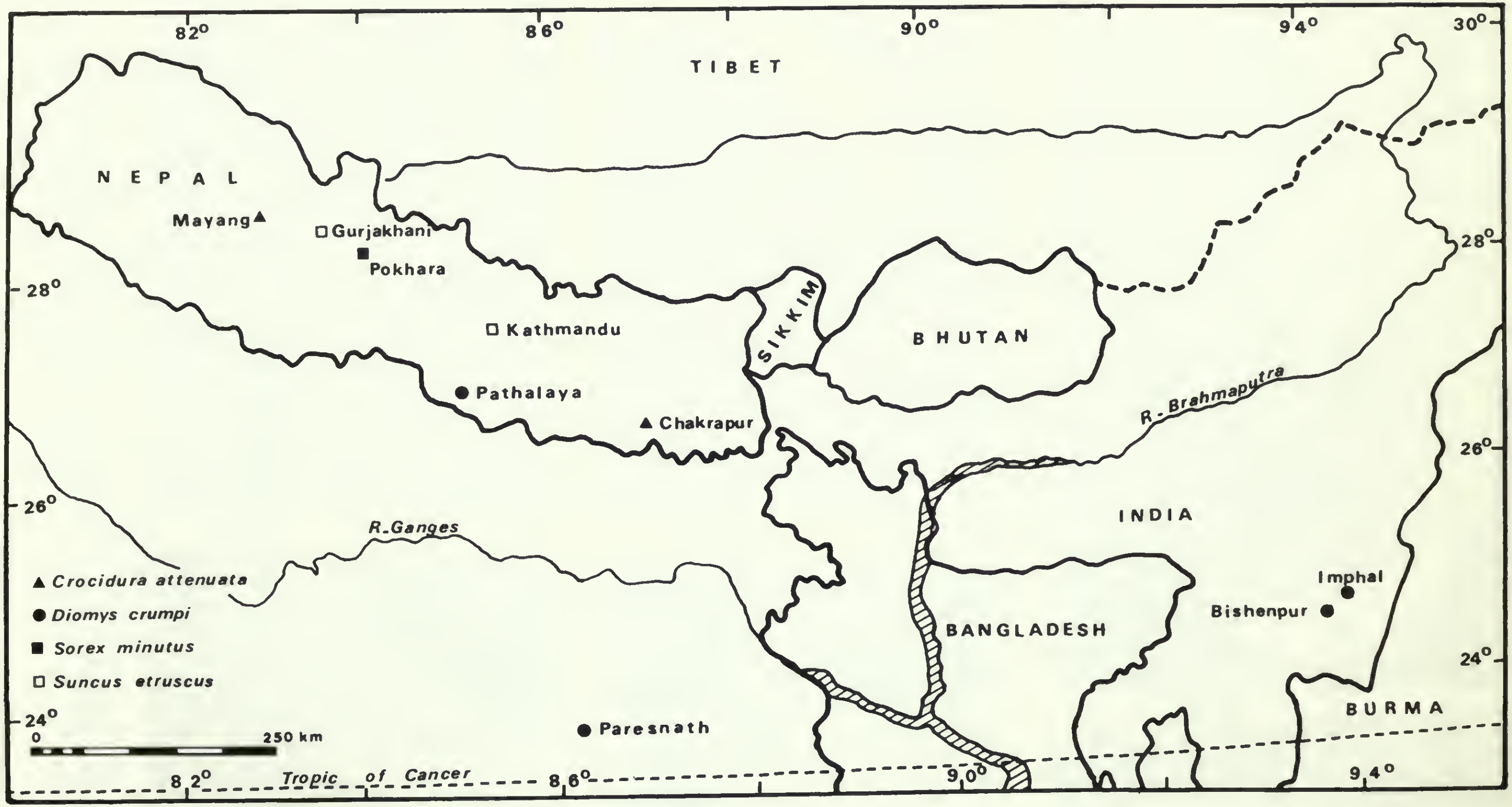
82°
86°
90°
94°
30°
28°
26°
24°
TIBET
NEPAL
Mayang ▲
☐ Gurjakhani
■ Pokhara
☐ Kathmandu
● Pathalaya
▲ Chakrapur
SIKKIM
BHUTAN
R. Brahmaputra
INDIA
BANGLADESH
Imphal ●
Bishenpur ●
BURMA
R. Ganges
● Paresnath
▲ Crocidura attenuata
● Diomys crumpi
■ Sorex minutus
☐ Suncus etruscus
0
250 km
Tropic of Cancer

Fig. 1 The known distribution of *Diomys crumpi* together with hitherto unpublished localities for three species of shrews.

Until 1979 no further specimens had been received at the B.M.(N.H.), nor had any records been found in published literature. According to Walker (1975) the only recorded material for *Diomys* is in London and so it seems of interest to record now that two skins and four skulls, the first specimens received for more than 33 years, extend the known range for this genus by about 885 km to the west. They were collected by the University of East Anglia Expedition to Nepal (members M. R. W. Rands, leader, P. N. Newton, C. G. R. Bowden and P. W. Brown) on 9 December 1978, 3 km east of Pathalaya, Bara District, Narayani Zone (27°10′N 85°00′E) in the central terai of Nepal on the edge of the Indo-Gangetic Plain, some 200 m above sea level (see map). Here sandy loam soils overlie unmetamorphosed Quaternary sediments (Sharma, 1977) and are heavily reworked by termites (*Isoptera* sp.). Annual precipitation totals 2000 mm, of which 90% falls during the monsoon, usually from mid June until the end of August (Dobremez *et al.*, 1973)

The specimens were caught in break-back traps baited with peanut butter, in sal forest, a moist deciduous forest type dominated by sal (*Shorea robusta*) but containing a wide variety of other species including *Terminalia* sp., *Adina cordifolia*, *Dillenia pentagyna* and *Mitragyne parviflora* (Dobremez *et al.*, 1973). Saplings between 1 m and 2·25 m in height are abundant. The shaded forest floor is sparsely covered with grasses and a few herbs, but many bare patches of soil remain. The area is utilized for domestic timber and remains largely free of domestic stock. *Rattus rattus* and *Mus cervicolor* were also collected in sal forest at this locality, which contrasts markedly with the habitat of *Diomys crumpi* recorded at the type locality, a 'rocky mountain top'.

No ecological data is available for the Frost specimens although the four from Imphal collected by Hake and Lawrence, (B.M.(N.H.) Nos 67.180–183) were from dry scrub slopes: oak [*Quercus*] is mentioned on one of these labels.

MEASUREMENTS. The available samples, apart from a good series from Bishenpur consist of the holotype, an incomplete skull from Paresnath [?], 4 ♂♂ from Imphal and four from Nepal: one ♂ (tail amputated in life), 2 ♀♀, one very old and the other without a skin, and one skull of unknown sex.

The measurements published by Ellerman (1961) could not be matched when compared with those made by J. M. I. therefore all the skulls of the *Diomys* available, including the young, were re-measured. Since the collection is apparently unique (Walker, 1975) it seems of value to illustrate with histograms the range and number of some of the measurements taken (Fig. 2).

NOTES. Ellerman (1961) stated that 'the upper incisors tend to be faintly grooved' but it seems more accurate to describe them as Thomas (1917) did in his type description when he said 'their front surface unusually roughened', in fact the anterior surface bears irregular longitudinal striations which become less obvious towards the tip, which is usually a paler yellow than the upper part of the incisor.

Ellerman (1961) keyed out *Diomys* and *Zelotomys* (African) together because they both have proodont incisors, but in *Zelotomys* the incisors are far more forward projecting than in *Diomys* in which they are nearly at a right angle to the molar row.

PARASITES. Siphonaptera were collected from two specimens of *Diomys crumpi*. One ♂ and one ♀ *Stivalius aporus* Jordan & Rothschild (1922 : 254) were taken from a young ♂ *Diomys* (B.M.(N.H.) No. 79.2114) and one ♀ flea of this species was found on an old ♀ *Diomys* (B.M.(N.H.) No. 79.2115) together with a single ♀ *Nosopsyllus simla* Jordan & Rothschild (1921 : 196).

Acarina were also collected from *Diomys* specimens B.M.(N.H.) Nos. 79.2114–2116 but identifications are not yet available.

Crocidura attenuata Milne Edwards, 1872

Crocidura attenuata Milne Edwards, 1872 : 263, pl. 38B, fig. 1, pl. 39A, fig. 2. Moupin, Szechuan, China.

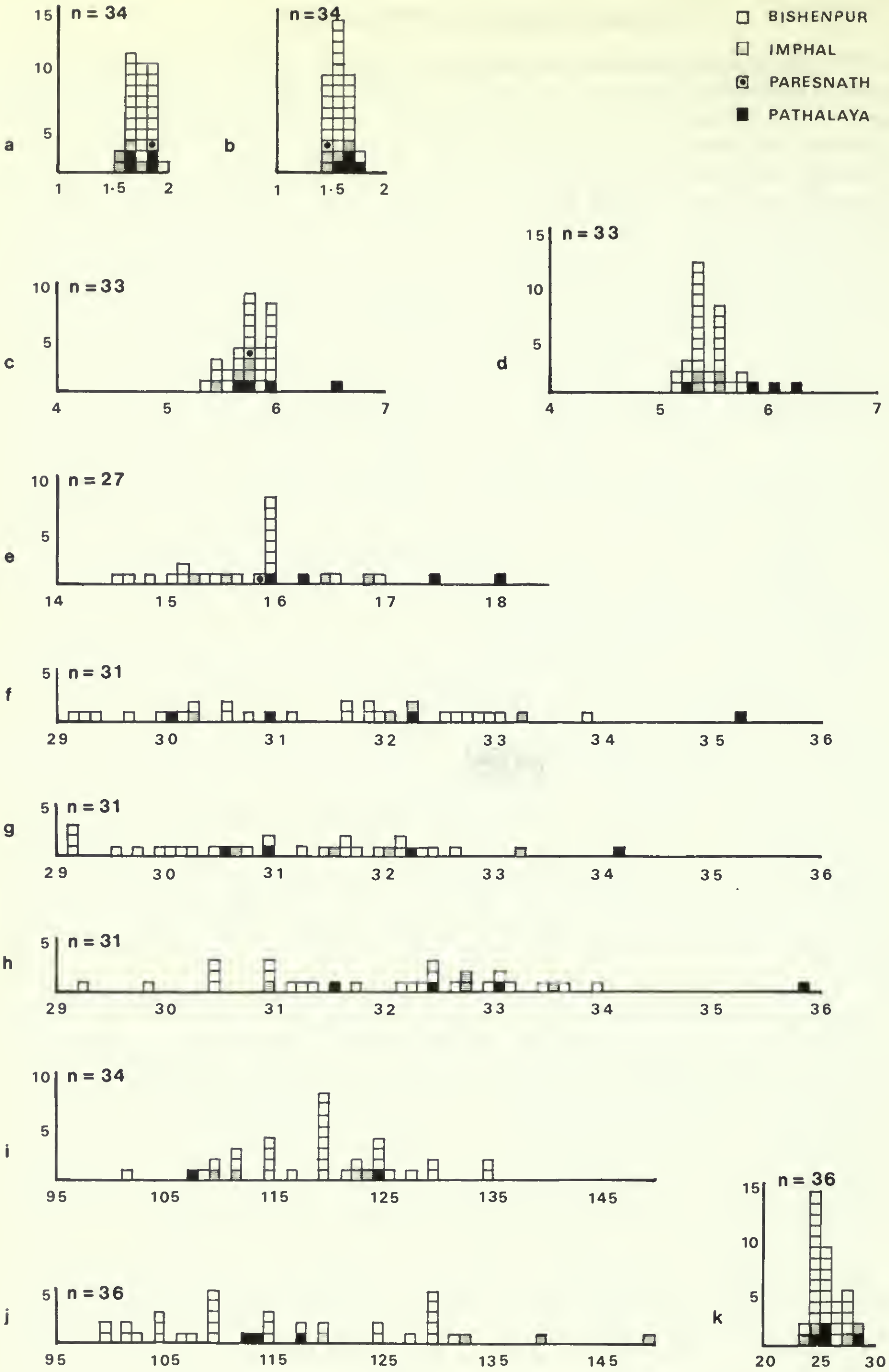

Fig. 2 Histograms of some measurements of the B.M.(N.H.) collection of *Diomys crumpi* including young specimens (x = measurement in millimetres; y = frequency). Skull measurements: a) maximum width m^1 b) maximum width m_2 c) alveolar length of upper molar row d) alveolar length of lower molar row e) zygomatic breadth f) condylobasal length g) occipito-nasal length h) greatest length. Skin measurements: i) tail j) head & body k) hind foot.

Crocidura grisea Howell, 1926 : 137. Seventy-five miles south-west of Yenpingfu, 500 ft, Fukien, China.

The first authenticated record of the species from Nepal was published by Mitchell and Punzo in 1976. The University of East Anglia Expedition collected three specimens in alcohol allocated to this species (B.M.(N.H.) Nos 79.997–999) from 3 miles south of Chakrapur, north of Fatepur on the west bank of the River Kosi, Diapurgarmi District, 26°50′N 87°01′E at about 300 m altitude. This is about 200 km S.E. of the Mitchell and Punzo locality.

A further specimen from Nepal in the B.M.(N.H.) collection was trapped by Dr G. B. Corbet of this museum when he was a member of the Royal Air Force Expedition to Dhaulagiri. The skin and skull of this single ♂ specimen No. 75.108, were collected from 2 miles N.E. of Mayang, south side of Pelma Khola, W. of Dhaulagiri at 28°39′N 82°50′E at an altitude of 6500 ft. on 11 April 1974. This specimen, which has proved difficult to allocate with certainty has four upper unicuspid teeth on each side which cast some doubt on its true identity, but Miss P. D. Jenkins, who has worked extensively on Asiatic *Crocidura* (1976) identified the U.E.A. expedition material, re-examined the specimen and came to the conclusion that it is an aberrant *C. attenuata*.

MEASUREMENTS. The measurements (in millimetres) of all the specimens of *Crocidura attenuata* from Nepal in the B.M.(N.H.) collection are listed below: those of the U.E.A. expedition, B.M.(N.H.) Nos 79.997–999 respectively, are followed by those of the aberrant specimen No. 75.108 enclosed in brackets.

Head & body: 61, 60·5, 65, (70); Tail: 60, 67·5, 63, (56); Hind foot: 12·5, 14·5, 15, (14·6); Ear: 8, 9·5, 9·5, (—).

Skull. Condylo-basal length: 18·6, 18·8, 18·1, (20·1); Greatest breadth across brain case: 8·4, 8·5, 8·3, (9·1); Least interorbital width: 4·0, 4·0, 3·9, (4·1); Length of upper tooth row: 8·0, 8·2, 7·9, (8·7); Width across m^2–m^2: 5·7, 5·9, 5·4, (5·9).

HABITAT. The single specimen collected by Dr Corbet was caught in dry scrub with *Berberis*, *Rhododendron* and *Quercus*.

The U.E.A. specimens were collected in an area of Recent sand and gravel deposits which is subject to regular flooding in the monsoon season and which receives an annual rainfall of 1500 mm (Sharma, 1977). The habitat is dominated by 'Elephant grass' but contains few other grass or herb species and no woody plants. The elephant grass varies in thickness and reaches a maximum height of 3 m. This riverine grassland, which is extensively grazed and trampled by domestic stock and in many areas frequently cut, is in danger of extinction in Nepal (Rands *et al.* 1980).

PARASITES. One ♂ and 2 ♀♀ fleas were collected from *Crocidura attenuata* specimens B.M.(N.H.) Nos. 79.997–999. They have been identified as *Acropsylla* ? *traubi* Lewis (1973 : 104).

No Acarina were collected from these specimens.

Suncus etruscus (Savi, 1822)

The first substantiated records for this species were published by Mitchell and Punzo in 1976 when nine specimens were recorded from two localities. Two further locality records are now provided from specimens in the B.M.(N.H.). They are No. 90.1.1.56 collected on 15 September 1877 at the 'Residency', Kathmandu [c. 27°43′N 85°19′E] by J. Scully and presented by W. J. Blanford and No. 55.73, a female collected on 8 July 1954 at Gurjakhani, 54 miles N.W. of Pokhara at 8500 ft, 28°36·5′N 83°13·5′E by Mr K. H. Hyatt when on a British Museum expedition. See Fig. 1.

The older specimen was assigned by Thomas to the species *hodgsoni* (Blyth, 1855). However, there appears to be some doubt about the correct name for *hodgsoni*, see Lindsay (1929) and Corbet (1978). Because of this the specimen was re-examined by J. M. I. and found to fit well within the range of measurements of specimens of *Suncus etruscus* from other regions and to key into the taxon according to the criteria used by Corbet, 1978. No attempt has been made to allocate to subspecies either of the specimens now listed.

No ecological details are available for these two specimens.

Sorex minutus Linnaeus, 1766

A specimen in the B.M.(N.H.) was mentioned by Corbet (1978) when he listed the distribution of the species. Since this appears to be the first authenticated record for Nepal it seems of value to give the details. This young ♀ specimen is B.M.(N.H.) No. 55.74 and was collected by hand in grass by Mr Hyatt on 18 August 1954 on a ridge about 18 miles N.E. of Pokhara, 28°22·5′N 84°7·5′E between 13,000 and 14,000 ft. See Fig. 1.

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A revision of the spider genera *Asemonea* and *Pandisus* (Araneae : Salticidae)

F. R. Wanless

Zoology series Vol 39 No 4 27 November 1980

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A revision of the spider genera *Asemonea* and *Pandisus* (Araneae : Salticidae)

F. R. Wanless

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Contents

Synopsis 213
Introduction 213
The genus *Pandisus* 217
  Definition 217
  Remarks 218
    Diagnosis 218
  Species list 218
  Key to species 218
The genus *Asemonea* 225
  Definition 225
  Diagnosis 226
  Species list 226
  Key to species 226
The genus *Goleba* 245
  Definition 245
  Diagnosis 245
  Species list 245
  Remarks 245
The *puella*-group 245
The *pallens*-group 249
Species Inquirenda 252
Acknowledgements 252
References 252

Synopsis

The spider genera *Pandisus* Simon and *Asemonea* O. P.–Cambridge are revised and one new genus *Goleba* is proposed. All 21 known species of these genera (of which 11 are new) are described and figured. Distributional data are given and a key to the species of *Pandisus* and *Asemonea* is provided. Generic relationships within the subfamily Lyssomaninae are discussed and generic groups based on the structure of the male genitalia are proposed. The type material of 11 nominate species was examined and five lectotypes are newly designated. Four specific names are newly synonymized and three new combinations are proposed.

Introduction

The present paper completes a series of generic revisions on old world Salticidae classified in the subfamily Lyssomaninae. Two genera, *Asemonea* O. P.–Cambridge and *Pandisus* Simon are revised and one new genus *Goleba* gen. n. is proposed.

The systematic position of lyssomanine spiders has been confused since Blackwall (1877) first proposed the formation of a separate family, the Lyssomanidae. In the same paper O. P.–Cambridge stated that although the genus *Lyssomanes* Hentz (type species *Lyssomanes viridis* (Walckenaer), Fig. 26A, B) is an exceedingly distinct and remarkable one there

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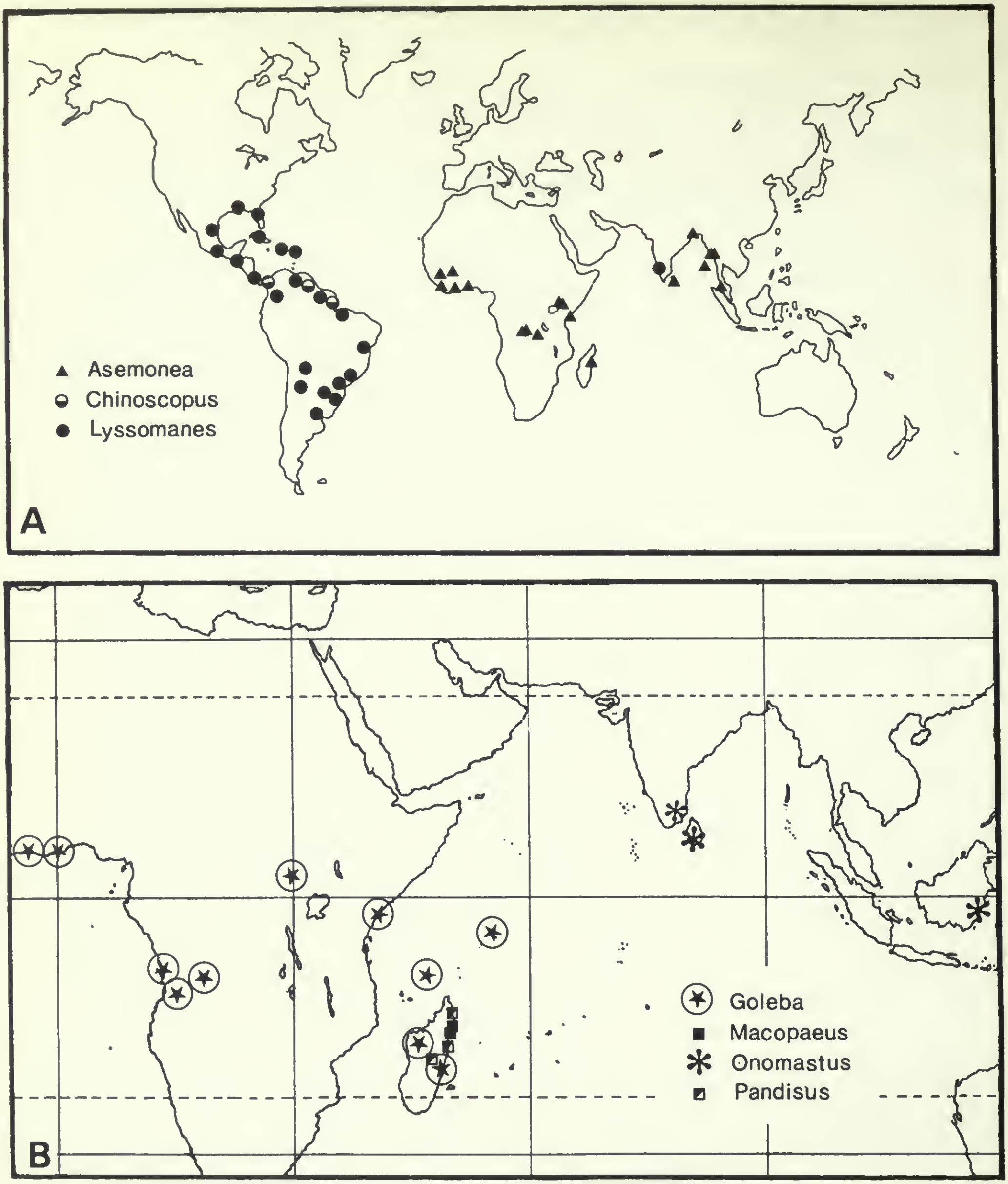

Fig. 1 A, distribution of *Asemonea, Chinoscopus* and *Lyssomanes*. B, distribution of *Goleba, Macopaeus, Onomastus* and *Pandisus*.

appears to be nothing to warrant its separation from salticids to which it is unmistakeably allied. The subsequent history of the lyssomanine has been reviewed by Galiano (1976), who redefined the group and concluded on morphological grounds that they merit no more than subfamilial rank within the Salticidae. Wanless (1978*b*) suggested that the lyssomanine were possibly related to several salticine genera (*Portia* Karsch, *Brettus* Thorell and *Cocalus* C. L. Koch) and that *Brettus* may have represented a possible link. However, this hypothesis could not be upheld when *Brettus* was revised (Wanless 1979). Subsequent studies (Wanless 1980a, b, c) have clarified, but not necessarily settled, the systematic position of several old world lyssomanine genera. *Onomastus* Simon, from Borneo, India and Sri Lanka is evidently not closely related to other lyssomanine genera. *Macopaeus* Simon, from Madagascar shows affinities with *Asemonea* and *Pandisus. Orthrus* Simon known only from three oriental species, belongs elsewhere on account of the structure of the secondary genitalia. *Lyssorthrus* Roewer, represented by a single species from New Guinea, seems to belong near the subfamily Boethinae and will be dealt with when those genera are revised. The Lyssomaninae (sensu Petrunkevitch, 1928) is therefore comprised of seven genera which, with the exception of *Lyssomanes,* have either a new or old world distribution (Fig. 1A, B):

Table 1 List of genera in the subfamily Lyssomaninae (sensu Petrunkevitch, 1928)

New world	Old world
Chinoscopus (5 species)	*Asemonea* (13 species)
Lyssomanes (54 species)	*Goleba* (3 species)
	Lyssomanes (1 species)
	Macopaeus (1 species)
	Onomastus (4 species)
	Pandisus (4 species)

According to Petrunkevitch, Caporiacco and other authors (Galiano 1976) there are two main diagnostic characters which distinguish lyssomanines from ordinary salticids: eyes in four rows and a tracheal system confined to the abdomen. As Galiano (1976) has already pointed out, recent findings (Esteban 1976) show that at least in some species of *Lyssomanes* there are tracheal tubes in the carapace. Wanless (1978*b*) argued that the degree of complexity of the tracheal system (i.e. simply or highly branched) was possibly of more evolutionary significance. However, recent studies (Wanless, in press e) on the trachea of *Hispo* Simon, a genus of ordinary salticids, has revealed a simple system resembling that found in *Asemonea tenuipes* O. P.-Cambridge. With regard to the eye arrangement, the statement 'eyes in four rows' is too imprecise and does not effectively define their pattern. It has already been shown (Prószyński 1968, Galiano 1976 and Wanless 1978*b*) that several genera of ordinary salticids (e.g. *Athamas* O. P.-Cambridge, *Synemosyna* Hentz, *Viciria* Thorell and *Mantisatta* Warburton) have the eyes arranged in four transverse rows. In spite of these difficulties and with reservations in respect of certain genera, Galiano (1976) redefined the subfamily on the basis of somatic characters. A reassessment of these characters and a comparative study of the secondary genitalia, especially the male palps, suggests that the subfamily is polyphyletic and comprised of Salticidae which have in most cases adapted to an arboreal existence associated with green leaves. For the present, I propose to divide the subfamily into three groups which can be defined on the basis of derived characters.

Group I. Comprised of one oriental genus, *Onomastus* Simon, which has recently been revised by the author (Wanless, 1980*c*). The synapomorphy linking all *Onomastus* species is the presence of a distinctive tegular apophysis not known to occur in other salticids. The placement of *Onomastus* remains uncertain as the palps are unusually complex and out-group comparison with *Oxyopes* (Family Oxyopidae, the supposed sister group of the Salticidae) suggests that they may have retained several characters (i.e. conductor and median apophysis) which have been secondarily reduced in many Salticidae (see Wanless 1980).

Group II. Includes two genera, *Lyssomanes* Hentz and *Chinoscopus* Simon. Both are distributed in the new world except for one species, *Lyssomanes karnatakaensis* Tikader & Biswas, from India (Fig. 1A). The species resemble one another in general habitus, but those of *Chinoscopus* are usually flatter and more elongate, also males lack the elongate chelicerae characteristic of *Lyssomanes*. The eye patterns are similar (Fig. 2A, B) and are presumed to

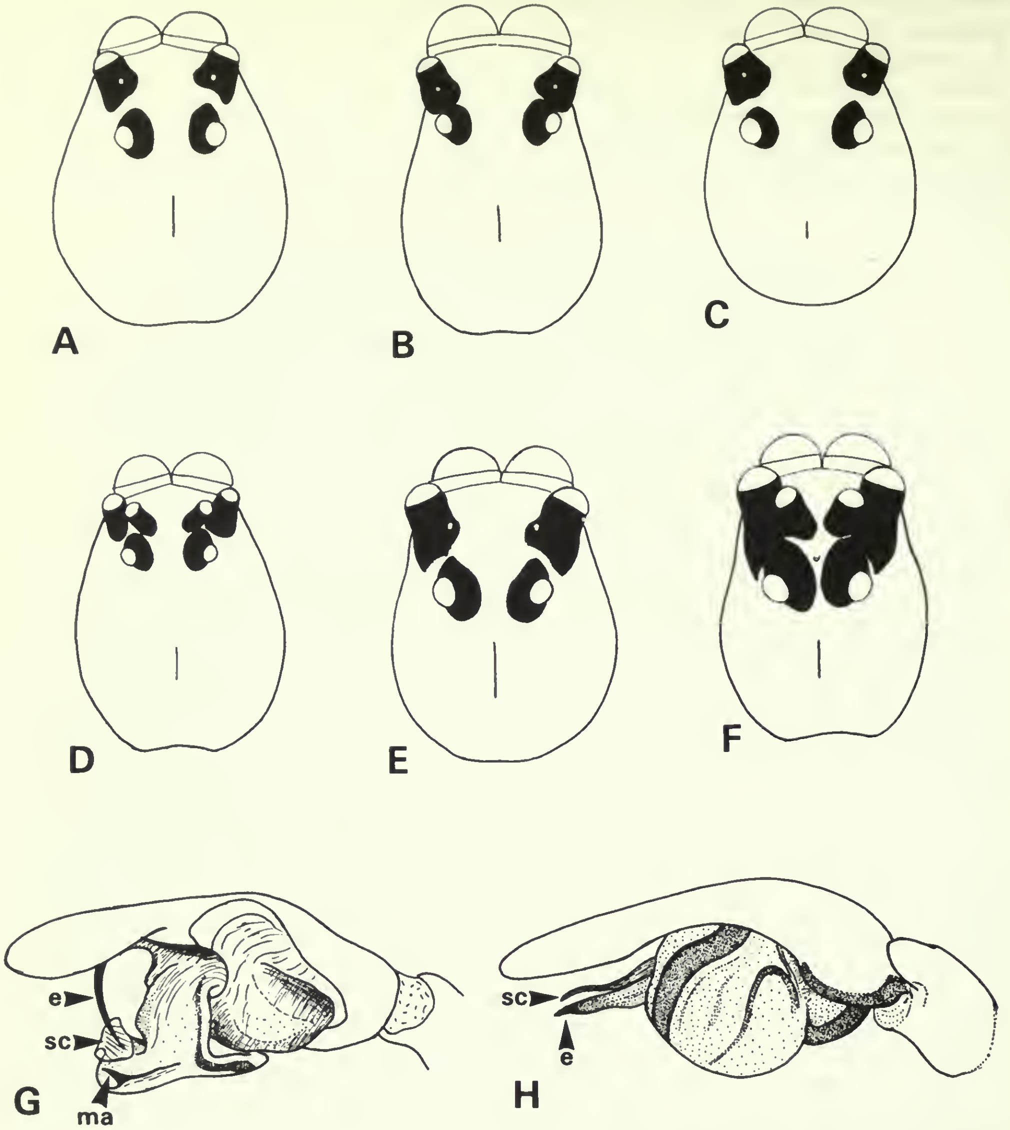

Fig. 2 (A–F) carapaces in dorsal view: A, *Lyssomanes viridus* (Walckenaer), ♂; B, *Chinoscopus flavus* Peckham, Peckham & Wheeler, ♂; C, *Onomastus patellaris* Simon, ♂; D, *Asemonea tenuipes* O. P.-Cambridge, ♂; E, *Pandisus sarae* sp. n., ♂; F, *Macopaeus spinosus* Simon, ♀. (G–H) ♂ palps ectal view: G, *Lyssomanes pencillatus* Mello-Leitão (after Galiano 1962); H, *Chinoscopus flavus.*

be derived in respect of other salticids. The male palps (Fig. 2G, H) are not unduly complex, but certain characters (i.e. membraneous secondary conductor (sc) and median apophysis (ma)) seldom occur in Salticidae. The occurrence of a membraneous conductor, fan-shaped in *Lyssomanes* and rod-like in *Chinoscopus,* may be synapomorphic for these genera, but at present I am uncertain as to the uniqueness of this type of conductor within the Salticidae. Furthermore, I am not sure if the median apophysis of *Lyssomanes* (evidently lacking in *Chinoscopus,* possibly as a result of secondary reduction) is homologous with that of *Onomastus.* My knowledge of *Lyssomanes* and *Chinoscopus* is too fragmentary for me to reach any firm conclusions on relationships concerning this group.

Group III. Known only from the old world and comprised of four genera, *Asemonea* O. P.-Cambridge, *Goleba* gen. n., *Macopaeus* Simon and *Padisus* Simon. The synapomorphy linking these genera is the migration of the posterior median eyes to a position closer to and clearly inside the optical axis of the anterior lateral eyes (Fig. 2D, E, F), the resulting pattern being different from that of all other known Salticidae.

The affinities of *Macopaeus* within this group are uncertain as the genus is only known from a single female specimen (Wanless, 1980*a*). Of the remaining genera, *Asemonea* and *Pandisus* are united by the presence of a ventral furrow and distal apophysis on the femora of the male palp (Figs 4E, 10E). They are presumed to be derived as such structures are not known to occur in any other Salticidae. The fourth genus, *Goleba* has been proposed for a group of species formerly included in *Asemonea* on account of close similarities in somatic characters, especially the eye dispositions. The male palps are however, clearly quite different (Figs 22D, E; 24B, E). The presence of a ventral tubercle on the palpal femora could be regarded as either germinal or vestigial in respect of the furrow and apical apophysis of *Asemonea* and *Pandisus,* but as the palpal tibial apophysis and sclerites are also distinctive it seems more likely that the ventral tubercle has been independently derived. If this is correct then *Goleba* probably evolved before the separation of *Asemonea* and *Pandisus.* The minute posterior median eyes of *Pandisus* may seem inconsistent with this hypothesis as these eyes are large in *Asemonea* and *Goleba.* However, their slightly elliptical outline suggests they may have been secondarily reduced.

The affinities between the *Asemonea* and *Lyssomanes* groups are uncertain. Similarities in respect of brooding behaviour and moulting (Eberhard 1974, Wanless 1978*b*, see also under *A. murphyi* sp. n., p. 23) suggests that they could be fairly closely related, but morphological characters, especially palpal structures, and distribution patterns indicate otherwise. They may even merit subfamily status. For the moment, I am reluctant to propose formal changes in classification as the relationships will possibly be more clearly understood when the subfamily Boethinae has been revised.

The measurements were made in the manner described by Wanless (1978*a*), but for the leg spination the system adopted is that used by Platnick and Shadab (1975).

Genus ***PANDISUS*** Simon

Lyssomanes: Peckham, Peckham & Wheeler, 1888 : 231 [in part].

Lyssomanes (*Maroussa*) Peckham, Peckham & Wheeler, 1888 : 225 [in part].

Pandisus Simon, 1900 : 27. Type species *Pandisus scalaris* Simon by original designation and monotypy. Simon, 1901 : 394, 397, 398. Petrunkevitch, 1928 : 181. Roewer, 1954 : 933; 1965 : 5. Bonnet, 1958 : 3322. Galiano, 1976 : 60.

DEFINITION. Small to medium spiders ranging from about 3·0 to 5·5 mm in length. Sexes alike in general habitus, sexual dimorphism sometimes evident in colour markings; not hirsute, leg fringes lacking. *Carapace:* longer than broad, moderately high with elevated eye region, widest at posterior margin of coxae II; fovea long and sulciform, positioned more or less midway between posterior lateral eyes and posterior thoracic margin; sculpturing not marked, cuticle sometimes weakly iridescent green. *Eyes:* with black surrounds except anterior medians; set on well developed tubercles; arranged in four transverse rows comprised of anterior medians, anterior laterals, posterior medians and posterior laterals; anterior medians largest, almost occupying full breadth of facies; anterior laterals more than half diameter of anterior medians, positioned behind and plainly wider than first row; posterior medians minute, sometimes slightly elliptical in outline, closer to and clearly situated inside optical axis of anterior laterals; posterior laterals as large or almost as large as anterior laterals, set closer together and well inside lateral margins of carapace; quadrangle formed by posterior median and posterior lateral eyes broader than long and widest posteriorly; entire quadrangle (measured from base of anterior median to posterior margin of posterior laterals) occupying between 46 and 52% of carapace length. *Clypeus:* between 38 and 52% of diameter of anterior median eyes; slightly concave with three or four curved setae in lower space between anterior median eyes. *Chelicerae:* of medium size, moderately robust, more or less vertical; promargin with three teeth, retromargin with seven to ten. *Maxillae:* moderately long, relatively broad, subparallel. *Labium:* subtriangular, about as long as wide and about half maxillae length. *Sternum:* broadly scutiform to cordiform. *Coxae:* subequal in size. *Abdomen:* elongate ovoid, colour markings generally inconspicuous, sometimes clothed in minute iridescent setae; anterior spinnerets robust, posteriors and medians slender, length subequal in males, posteriors slightly more elongate in females; position of colulus indicated by transverse row of 10 to 15 setae with a patch of setae anteriorly; anal tubercle a moderately well developed cone; tracheal system not examined. *Legs:* long and slender; spines numerous, long and robust; claws pectinate, tufts present, scopulae absent. *Female palps:* long and slender with apical claw. *Male palps:* complex, generally similar in form. Femora with ventral furrow fringed in setae, opening into apical apophysis; patellae usually with retrolateral apophysis; tibiae with retrolateral and dorsal apophyses; cymbium moderately long, sometimes with distal finger-like extension, clothed in long fine hairs (not always included in the figures); embolus (e) moderately long slender and curved, arising from basal margin of tegulum (t), detached from embolic guide (eg) but resting distally in a median tegular groove; pars pendula (p) sometimes present; tegulum somewhat bulbous, retrolateral margin sclerotized and grooved forming the embolic guide; subtegulum bulbous with sinuous ducts and scale-like apophysis (m). *Epigyne:* openings slit-like or broad with protruding median septum; introductory ducts diverge laterally from openings, looping and forming distal spirals; spermathecae ovoid with lanceolate fertilization ducts. Precise conformation of introductory ducts and their association with the spermathecae is uncertain.

REMARKS. The modified palpal femora probably secrete a fluid as there is evidently a duct in the apical apophysis (more apparent in *Asemonea*). It is not known if these modifications are in any way homologous with the ducted, male palpal tibial apophyses found in *Brettus* Thorell (Wanless 1979).

DIAGNOSIS. *Pandisus* is easily distinguished from *Asemonea, Goleba* and *Macopaeus* by the minute posterior median eyes and secondary genitalia.

List of species in the genus *Pandisus* Simon, 1900

Pandisus decorus sp. n.
P. modestus (Peckham, Peckham & Wheeler, 1888)
P. parvulus sp. n.
P. sarae sp. n.
P. scalaris Simon, 1900

Key to species of *Pandisus*

Males (males of *modestus* are unknown)

1	Palpal patella with retrolateral apophysis (Figs 3, 4D, 5C)	2
–	Palpal patella without retrolateral apophysis (Fig. 7C)	***parvulus*** sp. n. (p. 225)
2	Retrolateral apophysis of palpal patella slender (Fig. 3) .	***scalaris*** Simon (p. 219)
–	Retrolateral apophysis of palpal patella broad (Figs 4D; 5C)	3
3	Pars pendula (p) present (Fig. 4D, G)	***sarae*** sp. n. (p. 219)
–	Pars pendula absent (Fig. 5C, F)	***decorus*** sp. n. (p. 221)

Females (females of *parvulus* and *scalaris* are unknown)

1	Epigynal opening keyhole-shaped (Fig. 6C)	***Modestus*** Simon (p. 222)
–	Epigynal opening otherwise	2
2	Arch of epigynal opening relatively broad with darker markings extending laterally (Fig. 4C)	***sarae*** sp. n. (p. 219)
–	Arch of epigynal opening relatively narrow with indistinct lateral markings extending posteriorly (Fig. 5E)	***decorus*** sp. n. (p. 221)

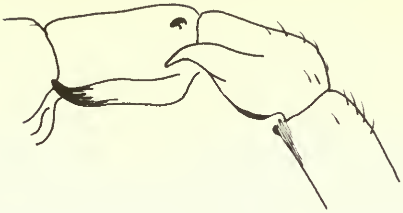

Fig. 3 *Pandisus scalaris* Simon, ♂ palp ectal view (after Simon 1901)

Pandisus scalaris Simon

(Fig. 3)

Pandisus scalaris Simon, 1900 : 27, ♂. [not examined, presumed lost]. Simon, 1901 : 391, 394, 396, 399. Petrunkevitch, 1928 : 181. Roewer, 1954 : 933; 1965 : 6.

REMARKS. Roewer (1965) examined, but did not describe the type specimen of this species which has subsequently been lost. Fortunately Simon (1900, 1901) provides a description and figure from which the species can be identified with some certainty.

DIAGNOSIS. *P. scalaris,* described only from the male, is distinguished from other known males of *Pandisus* by the long curved apophysis on the palpal patella (Fig. 3).

FEMALE. Unknown.

MALE (after Simon, 1900). Length 5·0 mm. Cephalothorax obscurely tawny, darkly margined, with ocular region on both sides broadly margined with black, clothed with brightly shining whitish green hairs. Clypeus at least twice as narrow as the anterior eyes and with shining hairs. Abdomen slender, yellow, above with a broad band including a pair of brick coloured spots, below on both sides marked with a long dark spot; above with shining white hairs, laterally, at least posteriorly with bright scarlet hairs. Chelicerae, mouth parts, sternum and coxae yellow. Legs obscurely tawny, with the anterior femora below broadly darkened and banded, armed with many long black spines. Palps tawny, with femora below and apically black and minutely pointed, with a short nodular patella armed below towards the lower margin with a black blade-like apophysis swollen basally, distally acute and hooked; tibiae a little longer than the patella, externally at the base almost dorsally with a small obtuse apophysis, on the lower margin with a larger black blade-like apophysis anteriorly subacute.

DISTRIBUTION. Madagascar, Tamatave.

REMARKS. This may be conspecific with *P. modestus.*

Pandisus sarae sp. n.

(Fig. 4A–J)

DIAGNOSIS. *P. sarae* is most closely related to *P. decorus,* but may be separated by the presence of a pars pendula (p) in males (Fig. 4D, G). Females are distinguished sometimes with difficulty by the broader epigynal arch (Fig. 4C) and apparent absence of posteriorly directed lateral markings.

MALE HOLOTYPE. *Carapace* (Fig. 4A–B): pale amber with darker margins and faint streaks radiating from foveal region; weakly iridescent. *Eyes*: with black surrounds except AM; AM sparsely fringed in pale yellowish hairs. *Clypeus*: tinged black with scattered iridescent setae (? rubbed). *Chelicerae*: light orange-brown, shiny with scattered long fine pale orange hairs; promargin with 3 teeth, retromargin with 8 or 9. *Maxillae and labium*: pale yellow tinged black. *Sternum* (Fig. 4I): pale yellow, thinly clothed in fine pale amber hairs. *Coxae*: pale

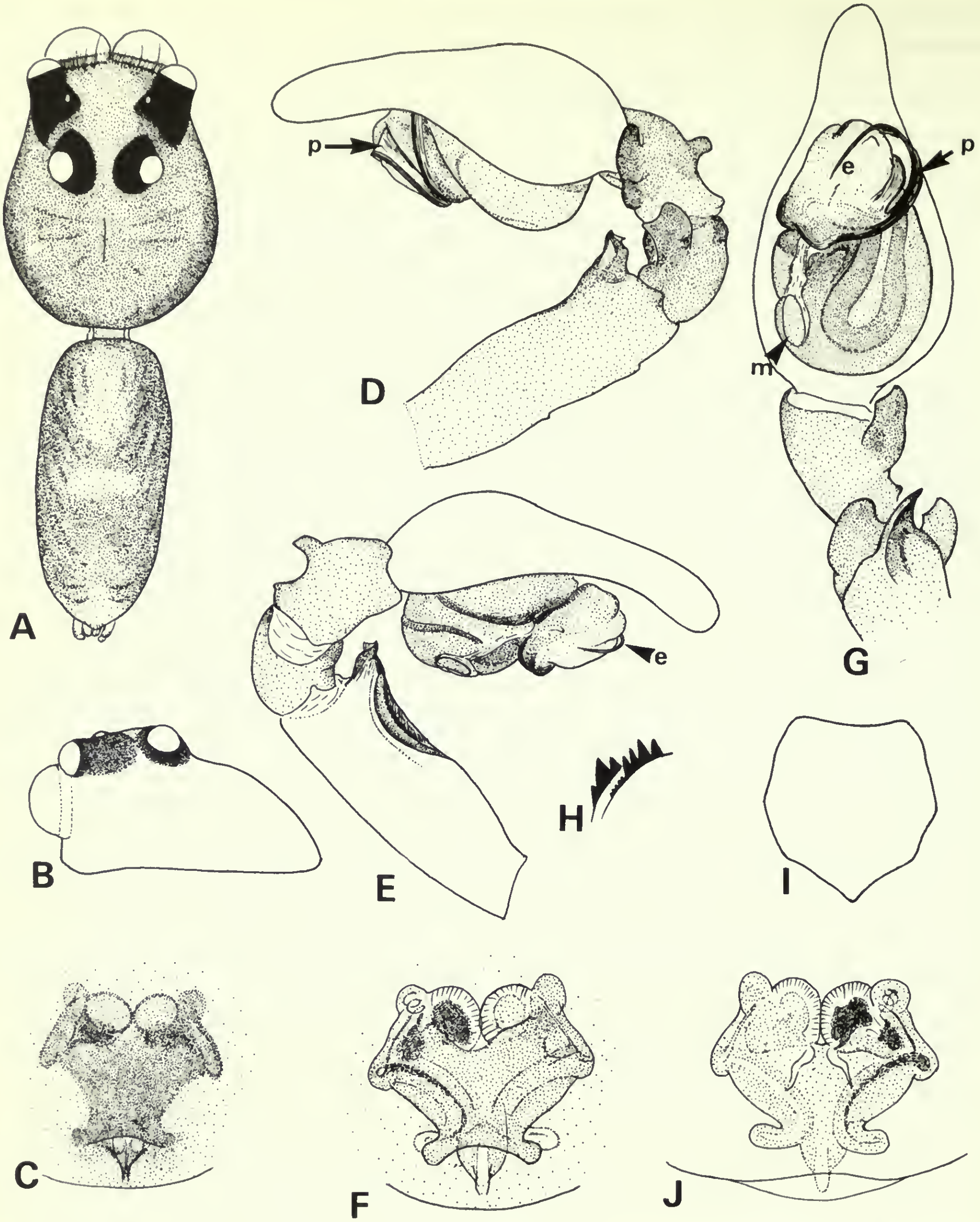

Fig. 4 *Pandisus sarae* sp. n., holotype ♂: A, dorsal view; B, carapace lateral view; D, palp, ectal view (= retrolateral view); E, palp, ental view (= prolateral view); G, palp, ventral view; H, cheliceral teeth; I, sternum. Paratype ♀: C, epigyne; F, vulva, ventral view; J, vulva, dorsal view.

yellow-brown. *Abdomen*: whitish yellow to greyish yellow with black markings; sparsely covered in fine pale amber hairs and minute iridescent setae; underside pale yellow with blackish lateral markings; spinnerets pale yellow lightly tinged black. *Legs*: yellow-brown grading to orange-brown distally with sides lightly tinged black. Leg I spines: metatarsi V 4–0–0, P 1–1–1, D 0–1–0, R 1–1–1, tibiae V 4–2–0, P 1–0–1, D 1–1–0, R 1–1–1; patellae R 0–1–0; femora P 0–1–1, D 1–1–1, R 0–1–1. *Palp* (Fig. 4D, E, G): pars pendula well developed.

Dimensions (mm): total length 4·96; carapace length 2·4, breadth 1·96, height 1·28; abdomen length 2·5; eyes, width of AM row 1·18, AL row 1·52, PM row 0·79, PL row 1·0; quadrangle length 1·08. *Ratios*: AM : AL : PM : PL : 14·5 : 8·5 : 2 : 8; AM : CL (clypeus) : 14·5 : 6.

FEMALE PARATYPE. Similar to ♂, but paler with less distinctive markings. General colouration whitish yellow to pale yellow with minute iridescent setae in eye region and blackish prolateral stripes on femora, patellae and tibiae of legs I and II. Spination of legs I: metatarsi V 4–0–0, P 1–1–1, D 0–1–0, R 1–1–1; tibiae V 4–2–0, P 2–1–0, D 1–1–0, R 1–1–1; patellae P 0–1–0, R 0–1–0; femora P 0–0–1, D 1–1–1, R 0–1–1. *Epigyne* (Fig. 4C, F, J): clothed in long whitish hairs. Lateral markings indistinct.

Dimensions (mm): total length 5·52; carapace length 2·44, breadth 2·0, height 1·36; abdomen length 2·92; eyes, AM row 1·32, AL row 1·6, PM row 0·8, PL row 1·16; quadrangle length 1·24. *Ratios*: AM : AL : PM : PL : 15·5 : 8·5 : 2 : 8·5; AM : CL : 15·5 : 8.

VARIATION. ♂ total length 4·88 to 5·12 mm, carapace length 2·4–2·56 mm (4 specimens); ♀ total length 5·3–5·52 mm, carapace length 2·32–2·44 mm (2 specimens). Males from Mt. Ambohisanga have iridescent setae (shining white under some angles of illumination) in eye region; the markings are less distinctive. In females the epigynes are sometimes plugged and as such cannot be readily separated from *P. decorus* sp. n.

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED. **Madagascar**: Beanana, holotype ♂, ii.1970 (*A. Lambillon,* MT. 142·599); paratypes 2 ♀♀, same data as holotype; Mt. Ambohisanga, paratypes 3 ♂♂, 1♀, i.1951 (*A. Pierrard,* MT. 142·914) (MRAC, Tervuren).

ETYMOLOGY. Named after my eldest daughter Sara Wanless.

Pandisus decorus sp. n.

(Fig. 5A–G)

DIAGNOSIS. *P. decorus* is most closely related to *P. sarae.* Males are readily distinguished by the apparent absence of the pars pendula, also by the shape of the retrolateral apophysis on the patella (Fig. 5C, F). Females are separated with difficulty by the narrower epigynal arch and lateral markings which extend posteriorly (Fig. 5E).

MALE HOLOTYPE. *Carapace* (Fig. 5A, B): yellow-brown with wide brown marginal bands; weakly iridescent with scattered iridescent setae in eye region. *Eyes*: with black surrounds except AM, anteriors sparsely fringed in dull yellowish hairs. *Clypeus*: yellow-brown tinged black, sparsely covered in fine iridescent hairs. *Chelicerae*: pale yellow, shiny; promargin with 3 teeth, retromargin with 7 or 8. *Maxillae and labium*: whitish yellow with sooty markings. *Sternum* (Fig. 5G): yellow-white, shiny. *Coxae*: pale yellowish. *Abdomen*: above pale yellow with grey-black markings, thinly clothed in fine iridescent hairs; underside whitish yellow with blackish sides; spinnerets pale yellow lightly tinged black. *Legs*: yellow-brown grading to orange-brown distally with lateral surfaces lightly tinged black. Leg I spines: metatarsi V 4–0–0, P 1–1–1, D 0–1–0, R 1–1–1; tibiae V 2–4–0, P 1–1–1, D 1–0–1, R 1–1–1; patellae P 0–1–0, R 0–1–0; femora P 0–0–1, D 1–1–1, R 0–1–1. *Palp* (Fig. 5C, D, F): pars pendula lacking.

Dimensions (mm): total length about 4·8; carapace length 2·24, breadth 1·82, height 1·31; abdomen length 2·44; eyes, width of AM row 1·28, AL row 1·64, PM row 0·82, PL row 1·12; quadrangle length 1·16. *Ratios*: AM : AL : PM : PL : 16 : 9·5 : 2·2 : 8·5; AM : CL : 16 : 6.

FEMALE PARATYPE. Similar to ♂, but more or less pale yellow in colour with scattered fine pale amber hairs (rubbed in ♂) and minute iridescent setae on abdomen. Leg I spines as in ♂

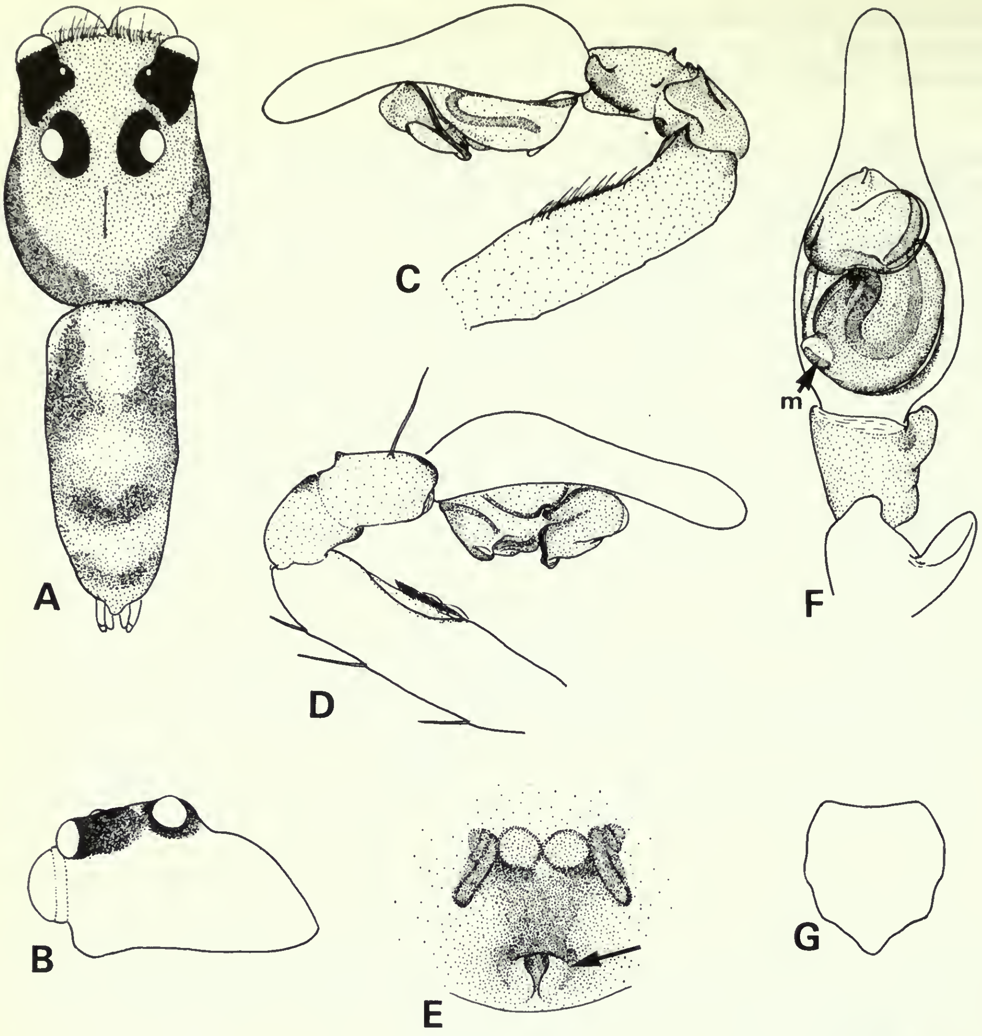

Fig. 5 *Pandisus decorus* sp. n., holotype ♂: A, dorsal view; B, carapace, lateral view; C, palp, ectal view; D, palp, ental view; F, palp, ventral view; G, sternum. Paratype ♀: E, epigyne.

except for the following: tibia V 4–2–0, P 1–0–1. *Epigyne* (Fig. 5E) similar to that of *P. sarae*.
Dimensions (mm): total length 5·3; carapace length 2·44, breadth 2·0, height 1·36; abdomen length 2·8; eyes, AM row 1·22, AL row 1·55, PM row 0·76, PL row 1·12; quadrangle length 1·16. *Ratios*: AM : AL : PM : PL : 15 : 9 : 2 : 8; AM : CL : 15 : 6.

Distribution. Madagascar.

Material examined. **Madagascar**: Est. Antsirabe, holotype ♂, paratype ♀, x.–xi.1970 (*J. Gossuin,* MT. 142·578) (MRAC, Tervuren).

Pandisus modestus (Peckham, Peckham & Wheeler)

(Fig. 6A–D)

Lyssomanes (Maroussa) modestus, Peckham, Peckham & Wheeler, 1888 : 231, ♀. LECTOTYPE ♀ and 8 ♀♀ PARALECTOTYPES (here designated) Madagascar (MCZ, Harvard) [examined].
Pandisus modestus: Simon, 1901 : 396. Roewer, 1954 : 933, 1965 : 6. Bonnet 1958 : 3322.

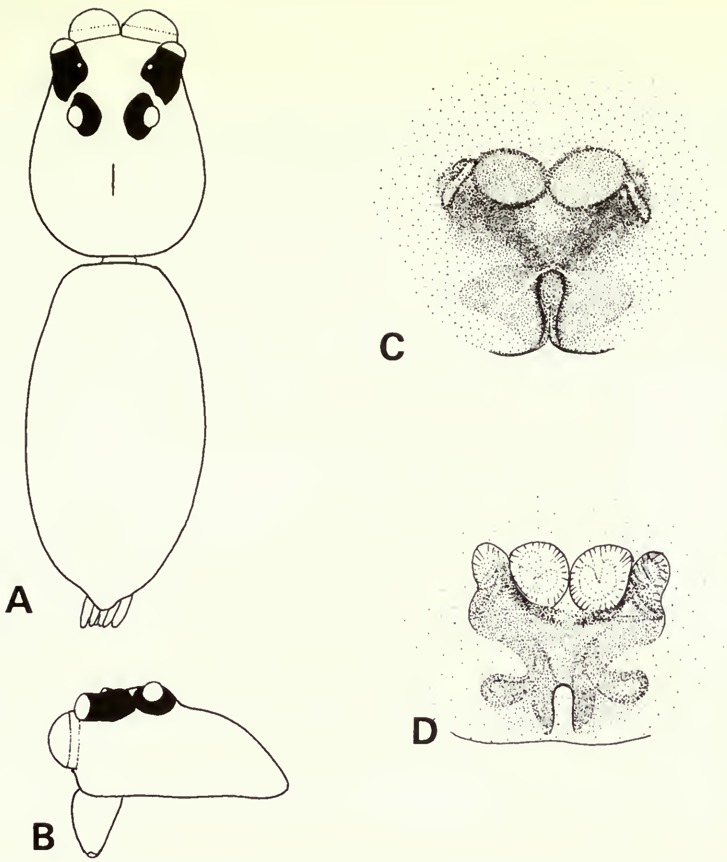

Fig. 6 *Pandisus modestus* Peckham, Peckham & Wheeler, lectotype ♀: A, dorsal view; B, carapace, lateral view; C, epigyne; D, vulva, ventral view.

Remarks. This species was originally placed in the subgenus *Maroussa* Peckham, Peckham & Wheeler, 1888 which was subsequently synonymized with *Lyssomanes* (Bonnet, 1957).

Diagnosis. *P. modestus* is distinguished from other species of *Pandisus* by the shape of the epigynal opening (Fig. 6C).

Male. Unknown.

Female lectotype. *Carapace* (Fig. 6A, B): yellow-brown, paler in eye region; weakly iridescent with scattered iridescent and dull whitish hairs in eye area. *Eyes*: with black surrounds except AM; AM sparsely fringed in light yellowish hairs. *Clypeus*: thinly clothed in fine whitish hairs. *Chelicerae*: pale yellow-brown, shiny; promargin with 3 teeth retromargin with 8. *Maxillae and labium*: whitish yellow with yellow-brown markings. *Sternum*: whitish yellow. *Coxae*: yellow-brown. *Abdomen*: yellow-brown with scattered pale amber hairs. *Legs*: yellow-brown with brownish sides on metatarsi and tibiae of legs I–II. Leg I spines: metatarsi V 4–0–0, P 1–1–1, D 0–1–0, R 1–1–1; tibiae V 2–4–0, P 2–0–1, D 1–0–1, R 1–1–1; patellae P 0–1–0, R 0–1–0; femora P 0–0–1, D 1–1–1, R 0–1–1. *Epigyne* (Fig. 6C, D).

Dimensions (mm): total length 5·0; carapace length 2·0, breadth 1·7, height 1·08; abdomen length 3·0; eyes, AM row 1·04, AL row 1·32, PM row 0·72, PL row 0·96; quadrangle length 0·92. *Ratios*: AM : AL : PM : PL : 12 : 7 : 2 : 6; AM : CL : 12 : 5.

Variation. ♀ total length 4·64 to 5·44 mm, carapace length 1·9–2·28 mm (9 specimens). As in other members of this genus the epigyne is sometimes plugged. However, the opening is nevertheless still fairly distinctive.

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED. Lectotype and paralectotype ♀♀, data as in synonymy.

REMARKS. This may be conspecific with *P. scalaris*, known only from the male.

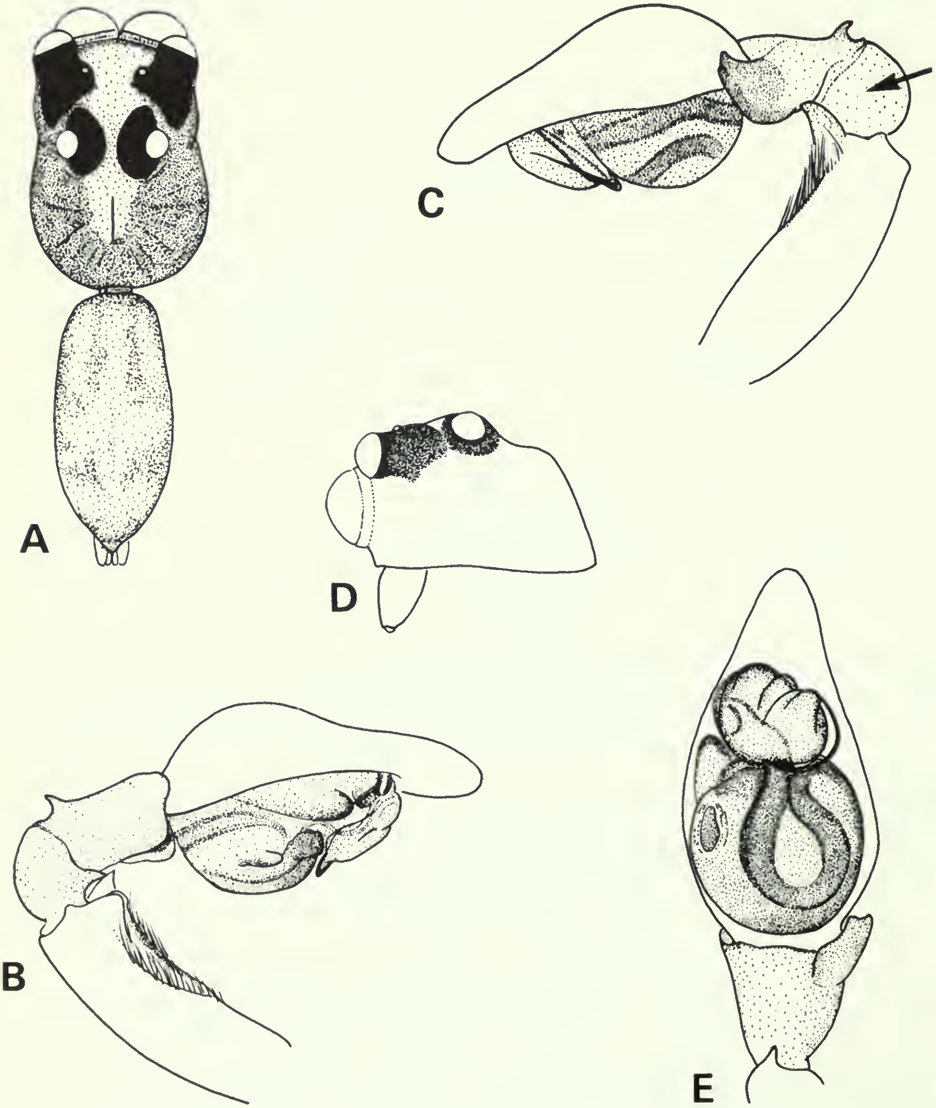

Fig. 7 *Pandisus parvulus* sp. n., holotype ♂: A, dorsal view; B, palp, ental view; C, palp, ectal view; D, carapace lateral view; E, palp, ventral view.

Pandisus parvulus sp. n.

(Fig. 7A–E)

DIAGNOSIS. *P. parvulus* is a small distinctive species readily separated from other species of *Pandisus* by the absence of a retrolateral apophysis on the palpal patellae (Fig. 7C).

FEMALE. Unknown.

MALE HOLOTYPE. *Carapace* (Fig. 7A, D): dark brown with eye and foveal regions whitish yellow and sooty markings radiating from fovea; glossy under some angles of illumination. *Eyes*: with black surrounds except AM. *Clypeus*: pale brown tinged black. *Chelicerae*: pale yellow with blackish markings; promargin with 3 teeth, retromargin with 7 or 8. *Maxillae and labium*: whitish yellow tinged black. *Sternum*: pale yellow, shiny. *Abdomen*: pale yellow with indistinct sooty markings; spinnerets pale yellow. *Legs*: pale yellow. Leg I spines: metatarsi V 2–0–0, P 1–2–1, R 1–2–1; tibiae V 2–4–0, P 2–0–1, D 0–0–1, R 1–0–1; femora P 0–0–1, D 1–1–2. *Palp* (Fig. 7B, C, E).

Dimensions (mm): total length 2·92; carapace length 1·44, breadth 1·07, height 0·92; abdomen length 1·44; eyes, AM row 0·83, AL row 0·98, PM row 0·4, PL row 0·68; quadrangle length 0·72. *Ratios*: AM : AL : PM : PL : 10·5 : 6·5 : 1 : 5; AM : CL : 10 : 4.

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED. **Madagascar**: Beparasy, holotype ♂, ii.1968 (*A. Lambillon*, MT. 142.739) (MRAC, Tervuren).

Genus ***Asemonea*** O. P.-Cambridge

Asemonea O. P.-Cambridge, 1869 : 65. Type species *Lyssomanes tenuipes* O. P.-Cambridge, by monotypy. Simon, 1901 : 382, 390, 391, 395, 397, 399. Petrunkevitch, 1928 : 181. Sherriffs, 1931 : 537. Gerhardt & Kästner, 1938 : 636. Bonnet, 1955 : 763. Galiano, 1976 : 59–67. Wanless, 1979 ; 184.

Asemonia: Waterhouse, 1902 : 34. Wanless, 1978b : 85, 86 [spelling mistake].

Asamonea: Simon, 1885 : 26. Peckham, Peckham & Wheeler, 1888 : 225, 241 [spelling mistake]. Roewer, 1954 : 927 [= *Asemonea* auct. alt.]; 1965 : 3.

Asamonia: Waterhouse, 1902 : 34 [spelling mistake].

DEFINITION. Small to medium spiders ranging from about 2·6 to 7·0 mm in length. Sexes alike in general habitus, sexual dimorphism sometimes evident in colour markings and presence of ornate fringes in males; distinctive colour patterns sometimes present. *Carapace*: longer than broad, low to moderately high with elevated eye region, widest at posterior margin of coxae II; fovea long, moderately sulciform, positioned more or less midway between posterior lateral eyes and posterior thoracic margin; sculpturing not marked, cuticle sometimes weakly iridescent green. *Eyes*: usually with black surrounds except anterior medians; set on moderately well developed tubercles; arranged in four transverse rows (rows two and three close) comprised of anterior medians, anterior laterals, posterior medians and posterior laterals; anterior medians largest, almost occupying full breadth of facies; anterior laterals about half or more than half diameter of anterior medians, positioned behind and plainly wider than first row; posterior medians relatively large, closer to and clearly situated inside optical axis of anterior laterals; posterior laterals almost as large as anterior laterals, set closer together and well inside lateral margins of carapace; quadrangle formed by posterior median and posterior lateral eyes broader than long and widest posteriorly; entire quadrangle (measured from base of anterior median eyes to posterior margin of posterior lateral eyes) occupying between 30 and 40% of carapace length. *Clypeus*: between 32 and 60% of diameter of anterior median eyes, sometimes clothed in fine shining hairs layered perpendicularly with three curved setae in lower space between anterior median eyes. *Chelicerae*: small to medium in size, moderately robust, vertical or inclined posteriorly; promargin with three, rarely two teeth, retromargin with five to seven, rarely three. *Maxillae*: of medium length, outer margins not deeply excavated; parallel or convergent. *Labium*: subtriangular, usually wider than long, about half or less than half maxillae length. *Sternum*: cordiform, margins usually indistinct. *Coxae*: subequal in size. *Abdomen*: slender to elongate ovoid; colour markings sometimes conspicuous; occasionally clothed in minute iridescent setae; spinnerets rarely subequal in length, posteriors usually longest with long terminal article; position of colulus sometimes indicated by three to four setae; anal tubercle a moderately well developed cone; tracheal system (of *A. tenuipes*) evidently simply branched and not protruding into cephalothorax. *Legs*: long and slender, fringes occasionally present; spines numerous, long and moderately robust; claws pectinate, tufts present, scopulae absent. *Female palps*: long and slender with apical claw. *Male palps*: complex, generally interspecifically distinct. Femora with ventral furrow, usually fringed in setae, opening into apical apophysis; patellae without apophyses; tibiae with dorsal and retrolateral apophyses, the latter usually anvil-shaped; cymbium moderately deep, fringed in long setae; embolus (e) long, curved and slender, arising from basal margin of tegulum, free from embolic guide, but resting distally in lateral tegular groove; tegulum (t) more or less ovoid in ventral view, margins modified to form embolic guide (eg) which is sometimes provided with distal flange (f); pars pendula apparently lacking; subtegulum (st) bulbus with sinuous ducts, occasionally with opaque whitish patch or swelling in region of apophysis (m) (c.f. *Pandisus*). *Epigynes*: variable in form. Atrium undivided, with median septum, or covered by median scape; introductory ducts, sometimes coiled; primary spermathecae more or less ovoid with lanceolate fertilization ducts; secondary spermathecae apparently lacking; tubular gland-like ducts sometimes present.

DIAGNOSIS. *Asemonea* is easily distinguished from *Pandisus* and *Macopaeus* by the eye pattern (Fig. 2D) and from *Goleba* by the presence of the palpal femoral furrow in males and by the appearance of the epigyne in females.

List of species in the genus *Asemonea* O. P.-Cambridge

Asemonea crinita sp. n.
A. cristata Thorell, 1895
A. fimbriata sp. n.
A. liberiensis sp. n.
A. maculata sp. n.
A. minuta sp. n.
A. murphyi sp. n.
A. ornatissima Peckham, Peckham & Wheeler, 1888
A. picta Thorell, 1895
A. pinangensis sp. n.
A. pulchra Berland & Millot, 1941
A. stella sp. n.
A. tenuipes O. P.-Cambridge, 1869

Key to species of *Asemonea*

Males (males of *liberiensis, orantissima* and *picta* are unknown)

1 Tegular flange (f) present (Fig. 1OF) 2
– Tegular flange absent (Fig. 15E) 5
2 Tibiae of legs I–II densely fringed in setae (Fig. 10C); palp as in Fig. 10B, E, F (Angola) . . . . ***fimbriata*** sp. n. (p. 229)
– Tibiae of legs I–II not densely fringed; palp otherwise 3
3 Palpal tibiae with dorsal peg-like spines (Fig. 19C) (Burma) . ***cristata*** Thorell (p. 242)
– Palpal tibiae without dorsal peg-like spines 4
4 Palpal tibiae with large complex dorsal apophysis (Fig. 13C) (Ivory Coast) ***maculata*** sp. n. (p. 233)
– Palpal tibiae with simple dorsal apophysis (Fig. 11C) (Kenya) . . ***murphyi*** sp. n. (p. 231)

5 Abdomen with hair tufts (Fig. 14A, B; 18A) 6

– Abdomen without hair tufts 7

6 Femoral apophysis elongate, curved and distally bifid (Fig. 18B, C) (Burma, India, Sri Lanka) . . . . ***tenuipes*** O. P. -Cambridge (p. 240)

– Femoral apophysis short and distally acute (Fig. 14C) (West Africa) ***crinita*** sp. n. (p. 234)

7 Femoral apophysis slender (Figs 9C, 11C, 21D) 8

– Femoral apophysis broad (Figs 15C, 16C) 9

8 Body with extensive black markings (Fig. 21A); femoral apophysis bent distally (Fig. 21D) (Malaysia). . . . . ***pinangensis*** sp. n. (p. 244)

– Body without extensive black markings (Fig. 9A); femoral apophysis gently curved (Fig. 9C) (Angola) . . . . ***minuta*** sp. n. (p. 228)

9 Abdomen light coloured with dorsal stellate marking (Fig. 16A, 28A); femoral apophysis with distal groove (Fig. 16C) (Kenya) . . . . ***stella*** sp. n. (p. 237)

– Abdomen with extensive black markings dorsally (Fig. 15A); femoral apophysis without distal groove (Fig. 15C) (West Africa) . . . . ***pulchra*** Berland & Millot (p. 234)

Females (females of *crinita, cristata, fimbriata, maculata, minuta* and *pinangensis* are unknown)

1 Epigynal atrium broad with pipe-like spermathecae and coiled ducts anteriorly (Fig. 8C) (West Africa) . . . . ***liberiensis*** sp. n. (p. 228)

– Epigyne otherwise 2

2 Epigyne with lens-shaped pouches medially and anteriorly (Fig. 18G–I) (Oriental region) . . . . ***tenuipes*** O. P.-Cambridge (p. 240)

– Epigyne otherwise 3

3 Epigyne with pronounced or recumbent scape (Figs 12A; 17C, D; 20C) 4

– Epigyne with median septum and marginal gland-like tubules (Figs 15F–H; 16E) . . 6

4 Scape lobe-like with median depression (Fig. 12A–C) (Kenya) . . ***murphyi*** sp. n. (p. 231)

– Scape broadly subtriangular (Figs 17C, D; 20C) 5

5 Epigyne with indistinct anterior depression (Fig. 17C, D) (Madagascar) . . ***ornatissima*** Peckham, Peckham & Wheeler (p. 239)

– Epigynal depression lacking (Fig. 20C) (Burma) . . . . . . ***picta*** Thorell (p. 243)

6 Eye region black with black bands extending to posterior thoracic margin, abdomen pale yellowish with extensive black dorsal markings (Fig. 15A) West and Central Africa) . . . . ***pulchra*** Berland & Millot (p. 234)

7 Eye region whitish yellow with black v-shaped mark on thoracic part, abdomen whitish yellow with two black dorsal markings anteriorly and distinctive stellate mark medially (Fig. 16A) (Kenya) . . . . ***stella*** sp. n. (p. 237)

Asemonea liberiensis sp. n.
(Fig. 8A–C)

DIAGNOSIS. *A. liberiensis* does not appear to be closely related to any other known species of *Asemonea* from whch it can readily be distinguished by the coiled epigynal ducts (Fig. 8C).

MALE. Unknown.

FEMALE HOLOTYPE. *Carapace* (Fig. 8A–B): pale amber to whitish yellow. *Eyes*: with black surrounds except AM. *Clypeus*: clothed in recumbent silky white hairs. *Chelicerae*: pale yellow with scattered fine pale yellowish hairs; promargin with 3 teeth, retromargin with 7. *Maxillae and labium*: pale yellow. *Sternum*: whitish yellow. *Coxae*: pale yellow. *Abdomen*: pale yellow with blackish markings; spinnerets robust, posteriors longest; pale yellow. *Legs*: pale yellow with black lateral spots on apices of tibiae II to IV and basal part of tibae IV; spines strong and numerous on legs I–II, but fewer and weaker on legs III–IV, anterior leg spines arising from dark spots. Spinnation of legs I: metatarsi V 4–2–0, P 0–0–1, R 0–0–1; tibiae V 4–4–0, P 0–0–1, R 0–0–1; femora P 0–0–1. D 1–1–1. *Epigyne* (Fig. 8C): posterior margin of atrium irregular.

Dimensions (mm): total length 4·6; carapace length 2·0, breadth 1·52, height 0·92; abdomen length 2·6; eyes AM row 0·96, AL row 1·22, PM row 0·78, PL row 0·84; quadrangle length 0·72. *Ratios*: AM : AL : PM : PL : 11·5 : 6 : 4 : 5; AM : CL 11·5 : 5.

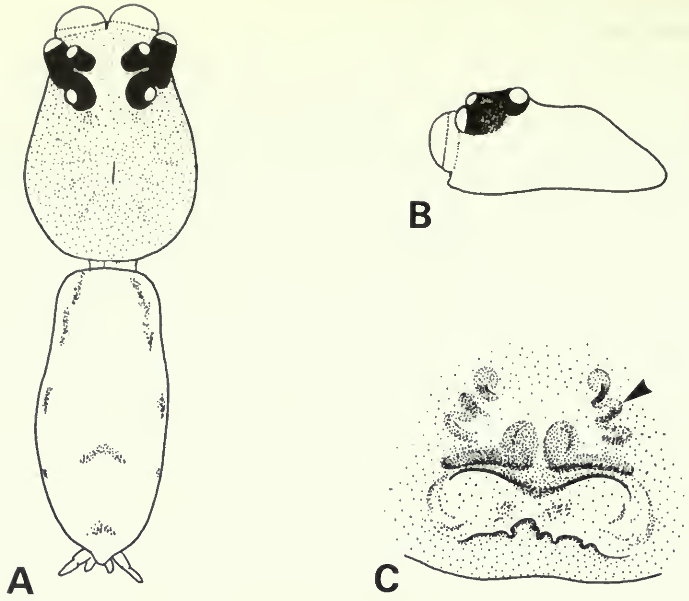

Fig. 8 *Asemonea liberiensis* sp. n., holotype ♀: A, dorsal view; B, carapace, lateral view; C, epigyne.

DISTRIBUTION. Liberia.

MATERIAL EXAMINED. **Liberia**, Pehata, holotype ♀, 1926 (*G. M. Allen,* R. P. Strong Exped., 1926) (MCZ, Harvard).

Asemonea minuta sp. n.
(Fig. 9A–E)

DIAGNOSIS. *A. minuta* is most closely related to *A. pinangensis,* from which it may be distinguished by the absence of heavy black markings (Fig. 9A), the shape of the femoral apophysis, the lack of a lip on the dorsal tibial apophysis (Fig. 9C) and distribution.

FEMALE. Unknown.

MALE HOLOTYPE. *Carapace* (Fig. 9A–B): pale yellow and weakly iridescent green with indistinct borderline and faint bands from PL to thoracic margin. *Eyes*: with black surrounds except AM; AM fringed in whitish hairs. *Clypeus*: whitish yellow with very obscure darker margins below AM. *Chelicerae*: whitish yellow, shiny; promargin with 2 teeth, retromargin with 3. *Maxillae, labium, sternum and coxae*: whitish yellow. *Abdomen*: pale yellow with faint longitudinal black bands; spinnerets pale yellow, posteriors longest with conical terminal article. *Legs*: whitish yellow; spines numerous, long and slender, but very pale. Spination of legs I: metatarsi V 2–4–0, P 0–0–1, R 0–0–1; tibiae V 2–4–2, D 0–1–0; femora P 0–0–1, D 1–1–1. *Palp* (Fig. 9C–E): small and lightly sclerotized.

Dimensions (mm): total length 2·6; carapace length 1·1, breadth 0·9, height 0·6; abdomen length 1·4; eyes, AM row 0·56, AL row 0·7, PM row 0·48, PL row 0·51; quadrangle length 0·44. *Ratios*: AM : AL : PM : PL : 6·5 : 3·1 : 2 : 2·5; AM : CL : 6·5 : 3.

DISTRIBUTION. Angola.

MATERIAL EXAMINED. **Angola**: Cacanda, holotype ♂, with sweep net, 23.ix.1946 (*A. de Barros Machado,* Ang. 30.2) (BMNH).

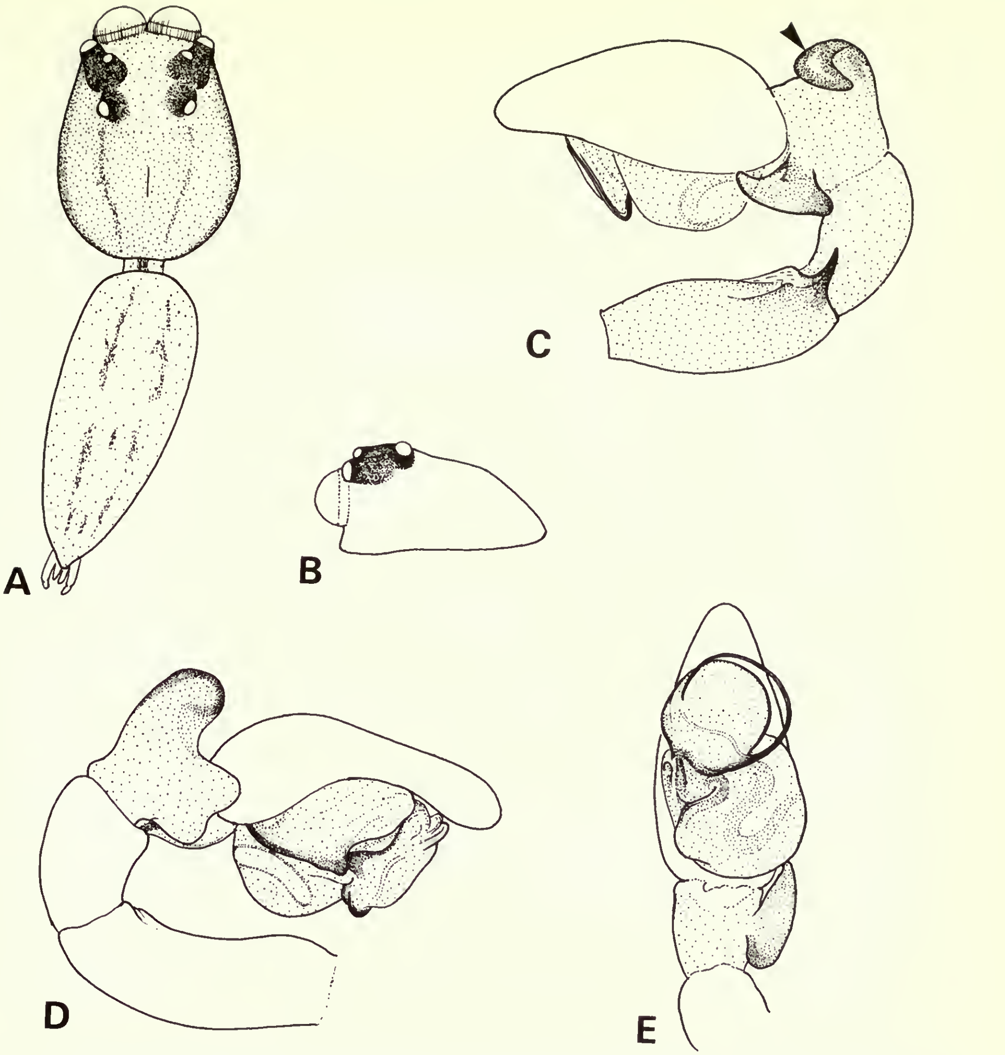

Fig. 9 *Asemonea minuta* sp. n., holotype ♂: A, dorsal view; B, carapace, lateral view; C, palp, ectal view; D, palp, ental view; E, palp, ventral view.

Asemonea fimbriata sp. n.

(Fig. 10A–F)

DIAGNOSIS. *A. fimbriata* is a distinctive species which seems to be most closely related to *A. murphyi*, but may be easily distinguished by the fringes of stiff hairs on tibiae I–II (Fig. 10C).

FEMALE. Unknown.

MALE HOLOTYPE. *Carapace* (Fig. 10A, D): pale amber with central whitish yellow band; thinly clothed in short dark amber hairs with scattered long pale yellow and silky white hairs in eye region. *Eyes*: with black surrounds except AM; AM fringed in whitish hairs. *Clypeus*: thinly clothed in fine whitish hairs. *Chelicerae*: pale yellow, shiny; promargin with 3 teeth, retromargin with 5. *Maxillae, labium, sternum and coxae*: pale yellow, shiny. *Abdomen*: pale yellow with vague blackish markings; thinly covered in erect amber hairs; spinnerets pale yellow thinly clothed in amber hairs, posteriors slightly longer than anteriors with

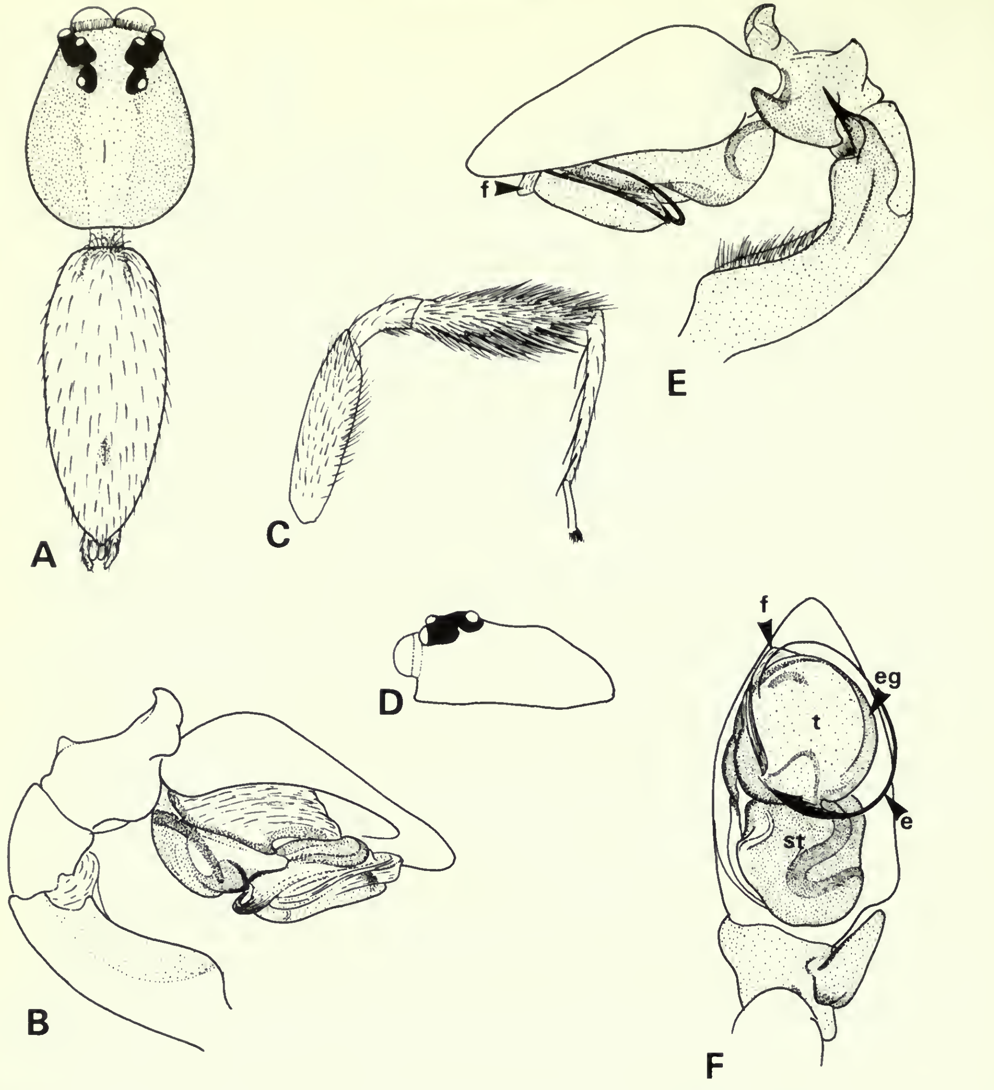

Fig. 10 *Asemonea fimbriata* sp. n., holotype ♂: A, dorsal view; B, palp, ental view; C, leg I; D, carapace lateral view; E, palp, ectal view; F, palp, ventral view.

conical terminal article. *Legs*: legs I–II pale yellow with tibiae and distal half of femora brownish, also dense black fringes on tibiae and underside of patellae; other legs yellowish with lighter femora and very scanty fringes on tibiae and patellae; spines long and numerous, pale to dark amber. Spination of legs I: metatarsi V 2–4–0, P 0–0–1, R 0–0–1; tibiae V 4–4–2; femora P 0–1–2, D 1–1–2. *Palp* (Fig. 10B, E, F): tegular flange (f) well developed.

Dimensions (mm): total length 4·6; carapace length 1·9, breadth 1·6, height 0·8; abdomen length 2·6; eyes, AM row 0·78, AL row 0·96, PM row 0·64, PL row 0·72; quadrangle length 0·56. *Ratios*: AM : AL : PM : PL : 10 : 5 : 3 : 3·7; AM : CL : 10 : 4·5.

DISTRIBUTION. Angola.

MATERIAL EXAMINED. **Angola**: Dundo, R. Mussungue, holotype ♂, 700 m, viii.1971 (*A. de Barros Machado,* Ang. 22734) (BMNH).

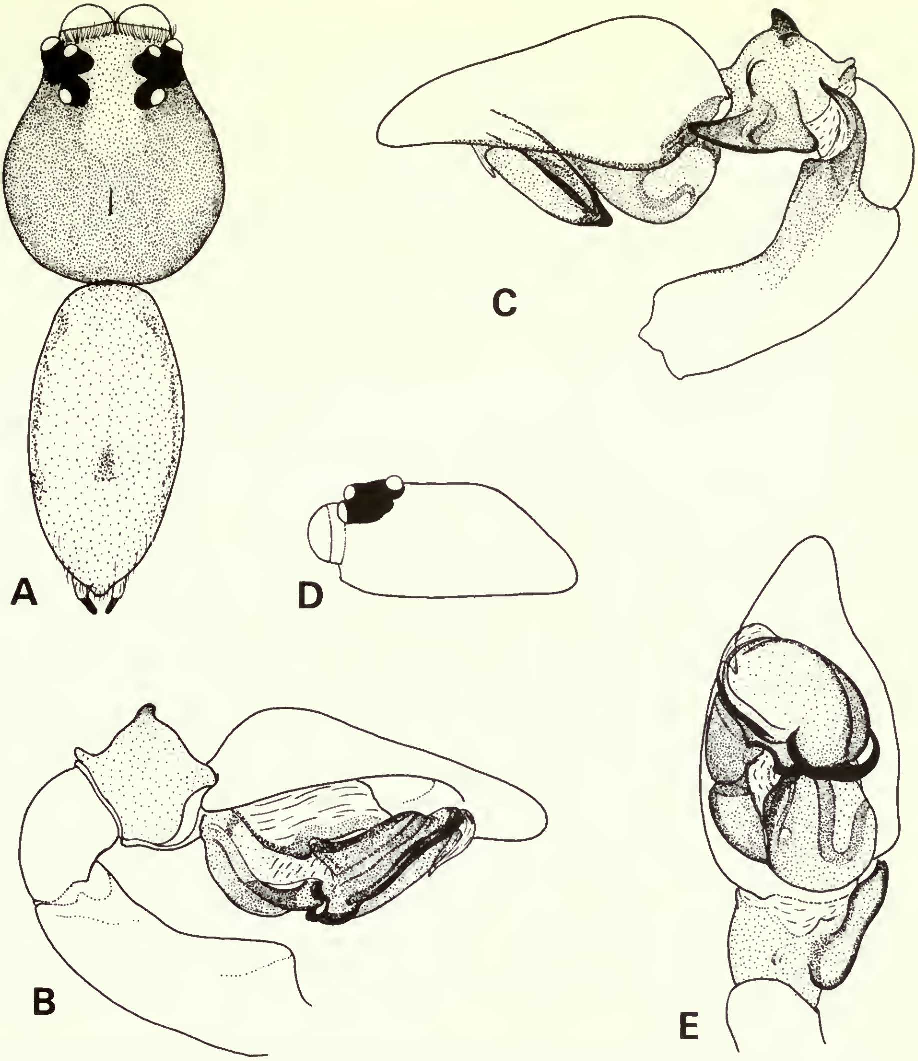

Fig. 11 *Asemonea murphyi* sp. n., holotype ♂: A, dorsal view; B, palp, ental view; C, palp, ectal view; D, carapace lateral view; E, palp, ventral view.

Asemonea murphyi sp. n.
(Figs 11A–E; 12A–C; 27A, B)

DIAGNOSIS. *A. murphyi* seems to be most closely related to *A. fimbriata*, but may be distinguished by the absence of fringes on legs I–II and palpal structure (Fig. 11B, C, E) in males. The epigyne (Fig. 12A–C) readily separates females of this species from other known species of *Asemonea.*

MALE HOLOTYPE. *Carapace* (Fig. 11A, D): yellow-brown, weakly iridescent green with eye region whitish and glossy under some angles of illumination, lateral margins lightly tinged black. *Eyes*: with black surrounds except AM; fringed in whitish hairs. *Clypeus*: pale yellow with sooty markings. *Chelicerae:* pale yellow basally tinged black; teeth not examined. *Maxillae, labium, sternum and coxae*: whitish yellow, shiny. *Abdomen*: pale yellow with faint sooty markings; sparsely clothed in long fine pale amber hairs; spinnerets pale yellow except for posteriors which have elongate black terminal articles. *Legs*: legs I whitish yellow

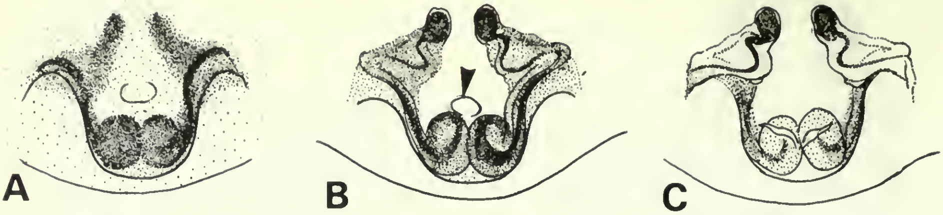

Fig. 12 *Asemonea murphyi* sp. n., paratype ♀: A, epigyne; B, vulva, ventral view; C, vulva, dorsal view.

to yellow-brown, tibiae grading to dark amber distally, also lateral sides of tarsi black, retrolateral sides of tibiae and femora with sooty stripes becoming black distally; other legs whitish yellow to yellow-brown with distal lateral spots on tibiae; spines strong and numerous. Spination of legs I: metatarsi V 2–2–1, P 1–0–2, R 1–0–2; tibiae V 2–2–2, P 1–0–1, D 1–1–0, R 0–1–1; patellae P 0–1–0, R 0–1–0; femora P 0–0–2, D 1–1–2. *Palp* (Fig. 11B, C, E): dorsal tibial apophysis bifurcate, best seen in posterior view.

Dimensions (mm): total length 3·92; carapace length 1·78, breadth 1·58, height 0·84; abdomen length 2·18; eyes, AM row 0·8, AL row 1·04, PM row 0·7, PL row 0·78, quadrangle length 0·54. *Ratios*: AM : AL : PM : PL : 10 : 4·4 : 3 : 4; AM : CL : 10 : 4·5.

FEMALE PARATYPE. *Carapace*: pale yellow grading to whitish yellow in eye region with irregular black spots on thoracic part, possibly remains of black bands that originally extended from PL to posterior margin. *Eyes*: with black surrounds except AM; densely fringed in creamy white hairs. *Clypeus*: pale yellow, shiny; sparsely clothed in fine whitish hairs. *Chelicerae*: yellow-brown, shiny; teeth not examined. *Maxillae and labium*: pale yellow. *Sternum and coxae*: whitish yellow, shiny. *Abdomen*: whitish yellow with scattered black spots and bars (more or less as in *A. maculata* sp. n.); spinnerets pale yellow, clothed in fine clear hairs; posteriors moderately elongate. *Legs*: whitish yellow to pale yellow-brown with apical and basal black spots on sides of tibiae I and retrolateral sides of tibiae II–IV; spines moderately strong, less numerous on posterior legs. Spination of legs I: metatarsi V 4–2–0, P 0–0–1, R 0–0–1; tibiae V 4–2–2, P 0–0–1; femora P 0–0–2, D 1–1–1. *Epigyne* (Fig. 12A–C): a small depression in central area of scape (similar depression also present in epigyne of *A. ornatissima*).

Dimensions (mm): total length 3·4; carapace length 1·52, breadth 1·2, height 0·8; abdomen length 1·96; eyes, AM row 0·68, AL row 0·92, PM row 0·6, PL row 0·67; quadrangle length 0·48. *Ratios*: AM : AL : PM : PL : 8·4 : 4·5 : 3 : 3·5; AM : CL : 8·4 : 4.

VARIATION. Paratype ♀ from Kitale 3·42 mm total length, 1·48 mm carapace length.

BIOLOGY. Captive specimens kept by Mrs F. Murphy all made a sheet web in the top of their cage in which they normally rested upside down. They all appeared to locate their prey by sight. One female laid several batches of two or three whitish green eggs which were place naked in the sheet web, unfortunately none of the eggs hatched, the first batch disappeared, presumably eaten. Although moulting was not observed several exuvia were seen hanging upside down below the sheet web. It seems reasonable to suggest that *Asemonea* species moult in the open and not inside a silken cell as is the case with many other salticids.

DISTRIBUTION. Kenya.

MATERIAL EXAMINED. **Kenya**: Naro Moru, beaten from shaded bushes on riverside path, 2000 m, holotype ♂, 17.viii.1974, taken alive, matured in captivity and killed 19.vi.1975 (*J. & F. Murphy,* 4336) (BMNH. 1979. 9.20.1); Kitale Forest, paratype ♀, beaten from low shrubs at edge of grassy track, 4.viii.1972 (*J. & F. Murphy,* 1549); Kitale Forest, paratype ♀, taken 22.vii.1974, died 1.ii.1975 (*J. & F. Murphy,* 3661) (BMNH).

ETYMOLOGY. This species is named after Mrs F. Murphy, London, who has helped me in various ways by providing photographs, rearing juvenile tropical salticids through to adulthood and allowing me to use her unpublished observations.

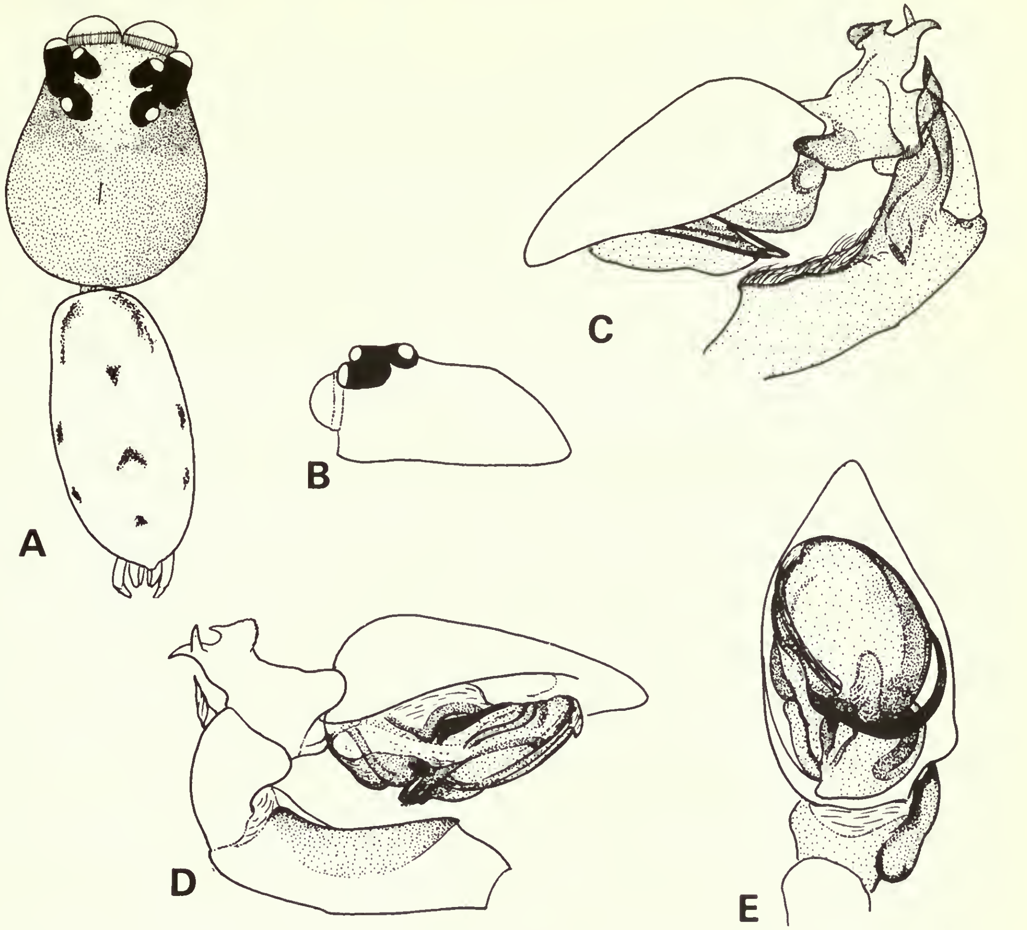

Fig. 13 *Asemonea maculata* sp. n., holotype ♂: A, dorsal view; B, carapace, lateral view; C, palp, ectal view; D, palp, ental view; E, palp, ventral view.

Asemonea maculata sp. n.

(Fig. 13A–E)

DIAGNOSIS. *A. maculata* is a distinctive species readily separated from other known species of *Asemonea* by the form of the grotesque palpal tibiae (Fig. 13C, D).

FEMALE. Unknown.

MALE HOLOTYPE. *Carapace* (Fig. 13A, B): pale amber grading to whitish yellow in eye region, glossy under some angles of illumination. *Eyes*: with black surrounds except AM; fringed in silky white hairs. *Clypeus*: pale yellow with sooty transverse band; thinly clothed in fine whitish hairs. *Chelicerae*: pale yellow with sooty markings; teeth not examined. *Maxillae and labium*: pale yellowish. *Sternum and coxae*: whitish yellow, shiny. *Abdomen*: whitish yellow with black spots; thinly clothed in very fine weakly iridescent setae; spinnerets whitish yellow, posteriors elongate with long terminal article. *Legs*: legs I whitish yellow with black tarsi and black lateral stripes on tibiae, patellae and femora; other legs whitish yellow with black streaks at either end of tibiae IV; spines strong and numerous. Spination of legs I: metatarsi V 2–4–2, R 1–0–0; tibiae V 4–4–0, P 0–0–1, D 0–1–0, R 0–0–1; femora P 0–0–1. D 1–1–2. *Palp* (Fig. 13C–E): tegular flange moderately well developed.

Dimensions (mm): total length 4·56; carapace length 2·08, breadth 1·8, height 1·04; abdomen length 2·4; eyes, AM row 1·0, AL row 1·28, PM row 0·82, PL row 0·88; quadrangle length 0·68. *Ratios*: AM : AL : PM : PL : 12 : 6 : 4 : 5; AM : CL : 12 : 6.

VARIATION. Paratype ♂ 4·7 mm total length, 2·10 mm carapace length.

DISTRIBUTION. Ivory Coast.

MATERIAL EXAMINED. **Ivory Coast**: environs of Kotiessou, R. Bandama, holotype ♂, from Bushes, (*J. Jezequell,* B3. 24) (MNHN, Paris). Paratype: 1♂, same data as holotype except vial B3.25, (BMNH).

Asemonea crinita sp. n.

(Fig. 14A–E)

DIAGNOSIS. *A. crinita* is an extraordinary looking species easily distinguished from other species of *Asemonea* by the palp (Fig. 14C–E) and ornate bent abdomen (Fig. 14A, B).

FEMALE. Unknown.

MALE HOLOTYPE. *Carapace* (Fig. 14A, B): amber grading to pale yellowish in eye region; thinly clothed in orange hairs on thoracic part. *Eyes*: with black surrounds except AM; fringed in fine silky white hairs. *Clypeus*: sparsely clothed in whitish hairs. *Chelicerae*: pale yellow; promargin with 3 teeth, retromargin with 4 or 5. *Maxillae and labium*: pale yellow. *Sternum and coxae*: whitish yellow, shiny. *Abdomen*: posteriorly bent; whitish yellow lightly tinged black; conspicuously fringed with tufts of coarse dark amber hairs; spinnerets pale yellow tinged black, posteriors elongate with long terminal article. *Legs*: pale yellow with blackish streaks on femora III–IV; spines moderately strong and numerous, but pale. Spination of legs I: metatarsi V 4–2–1, P 1–0–1, R 1–0–1; tibiae V 4–2–0, P 0–1–1, D 0–1–0, R 0–1–1; patellae P 0–1–0, R 0–1–0; femora P 0–0–2, D 0–1–1. *Palp* (Fig. 14C–E): tegular flange evidently lacking.

Dimensions (mm): total length 5·2 mm; carapace length 1·68, breadth 1·52, height 0·92; abdomen length 3·56; eyes, AM row 1·0, AL row 1·28, PM row 0·84, PL row 0·94; quadrangle length 0·62. *Ratios*: AM : AL : PM : PL : 12·5 : 6 : 4 : 5; AM : CL : 12·5 : 4.

VARIATION. Paratype ♂ from Lamto 5·3 mm total length, 1·68 mm carapace length. As both the holotype and paratype specimens have the abdomen posteriorly bent it is assumed that this is a natural condition and not an artifact of preservation.

DISTRIBUTION. Ivory Coast.

MATERIAL EXAMINED. **Ivory Coast**: environs of Kotiessou, R. Bandama, holotype ♂, (*J. Jezequel*, B6.14) (MNHN, Paris). Paratype: 1♂, same data as holotype except vial B6. 1, (BMNH).

Asemonea pulchra Berland & Millot

(Fig. 15A–H)

Asemonea pulchra Berland & Millot, 1941 : 401, ♂. Holotype ♂, Mali (MNHN, Paris) [examined]. Clark, 1974 : 12.

Asamonea pulchra: Roewer, 1954 : 927, 1965 : 4 [unjustified emendation].

DIAGNOSIS. *A. pulchra* is closely related to *A. stella*, but may be readily distinguished by the distinctive black markings (Fig. 15A) and absence of a distal furrow on the palpal femoral apophysis (Fig. 15B, arrowed). The epigynes, which are sometimes plugged, are very similar and cannot always be distinguished with certainty.

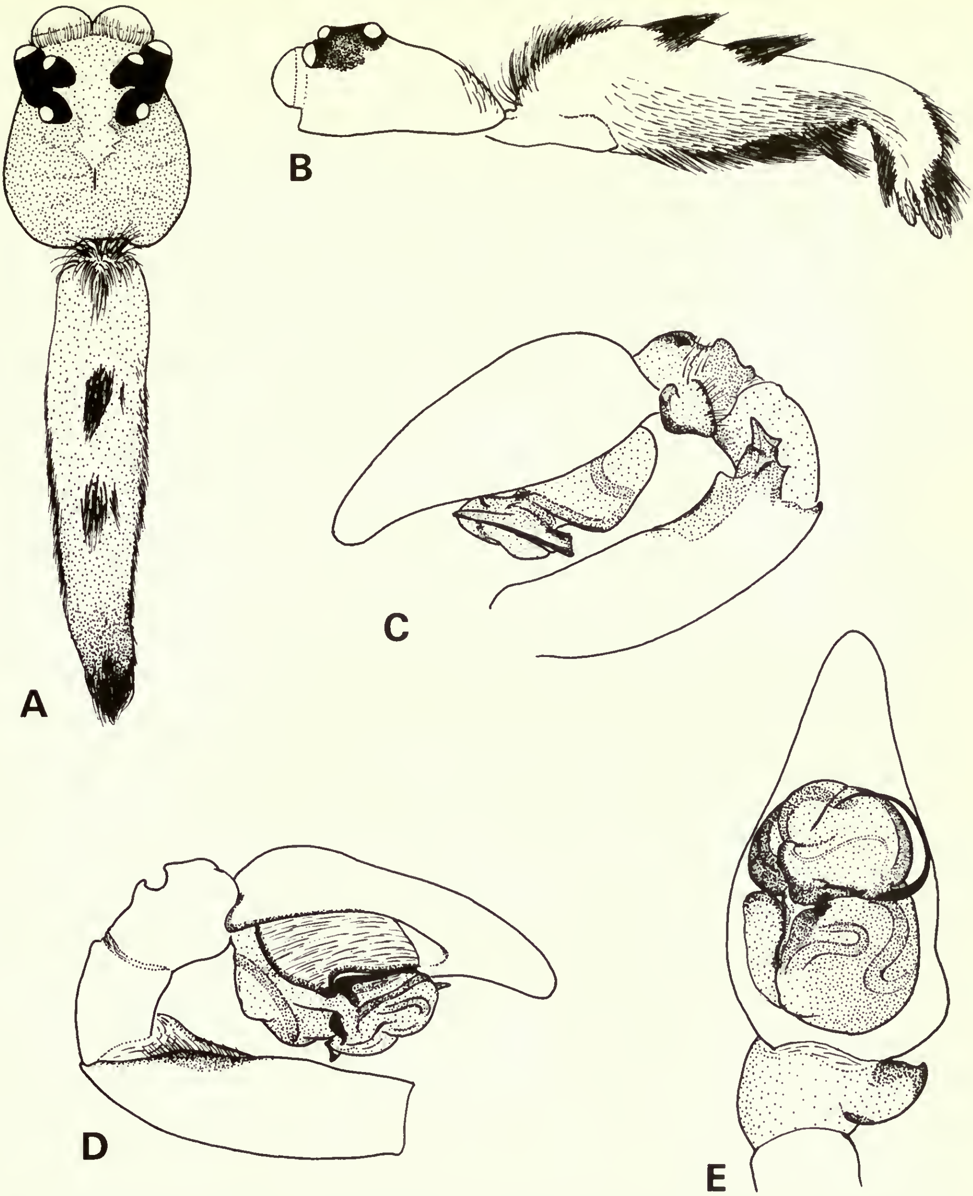

Fig. 14 *Asemonea crinita* sp. n., holotype ♂: A, dorsal view; B, lateral view; C, palp, ectal view, D, palp, ental view; E, palp, ventral view.

MALE HOLOTYPE. *Carapace*: whitish yellow with blackish eye region and black bands extending from posterior lateral eyes to posterior thoracic margin, the bands weakly iridescent green under some angles of illumination. *Eyes*: with black surrounds; fringed in whitish hairs. *Clypeus*: whitish yellow with black transverse band. *Chelicerae*: pale yellow, shiny, teeth not examined. *Maxillae, labium, sternum and coxae*: whitish yellow. *Abdomen*: yellow-brown tinged black with black markings; thinly clothed in long clear yellow-brown hairs; spinnerets black, fringed in brownish hairs, posteriors elongate with moderately long terminal article. *Legs*: legs I whitish yellow with black tarsi and black lateral stripes on patellae and either end of tibiae; legs II–IV similar, but tarsi pale yellowish and femora IV

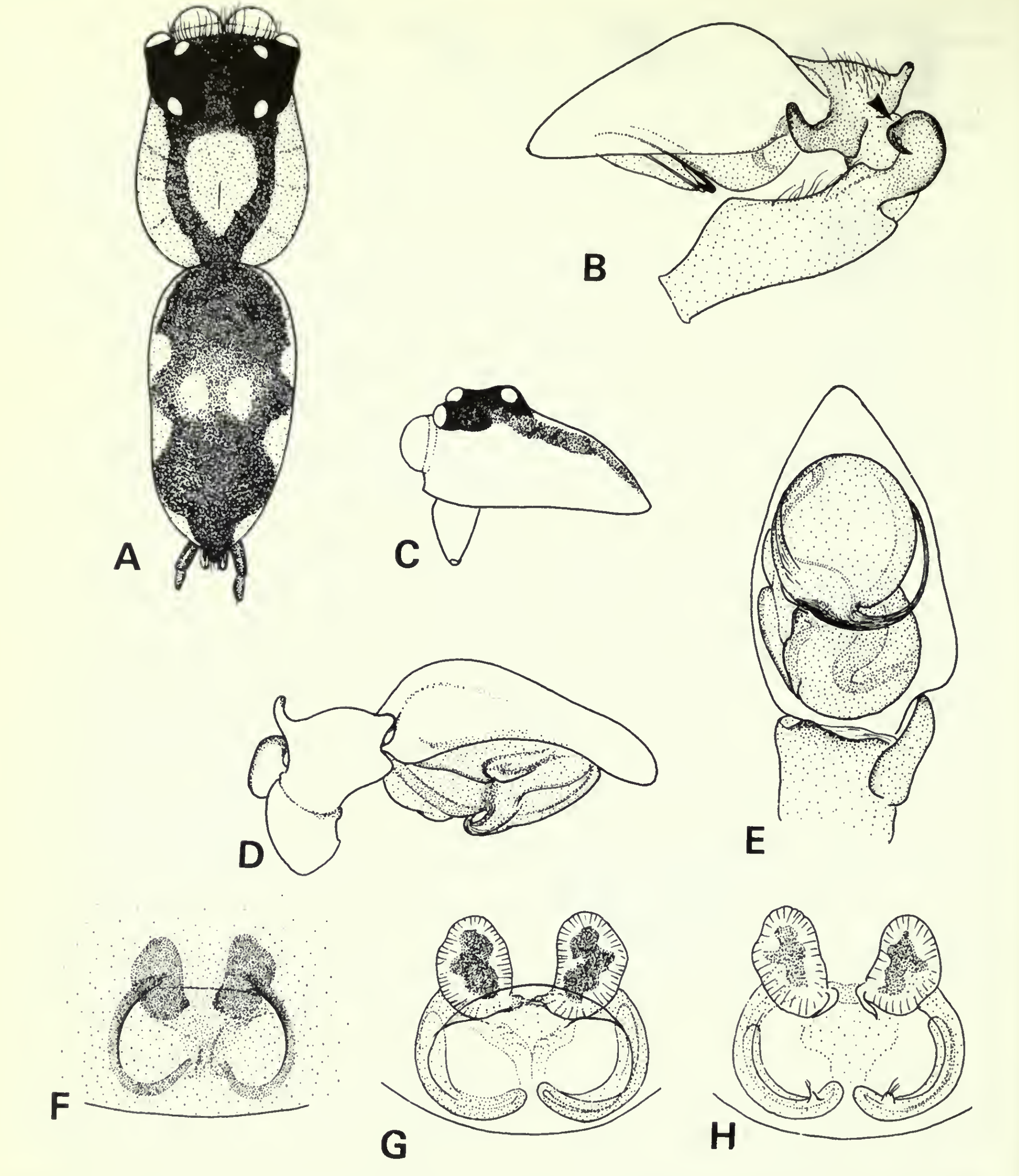

Fig. 15 *Asemonea pulchra* Berland & Millot, holotype ♂: B, palp, ectal view; D, palp, ental view; E, palp, ventral view. ♀ from Guinea: A, dorsal view; C, carapace, lateral view; F, epigyne; G, vulva, ventral view; H, vulva, dorsal view.

with apical black spots; spines moderately numerous and long, rather pale. Spination of legs I: metatarsi V 2–2–2, P 0–0–1, D 0–1–0, R 0–0–1; tibiae V 2–2–2, P 1–0–1, R 1–0–1; femora P 0–0–2, D 0–1–1, R 0–0–1. *Palp* (Fig. 15B, D, E): tegular flange lacking.

Dimensions (mm): total length 3·16; carapace length 1·4, breadth, 1·08, height 0·7; abdomen length 1·76; eyes, AM row 0·66, AL row 0·87, PM row 0·53, PL row 0·6; quadrangle length 0·44. *Ratios*: AM : AL : PM : PL : 8 : 4·5 : 3·2 : 3·5; AM : CL : 8 : 4.

FEMALE from Guinea (Fig. 15A, C). Similar to ♂ except for the following: *Clypeus*: pale yellow with black spot in lower space between AM; clothed in fine shining hairs. *Abdomen*: pale yellow with black dorsal markings; posterior spinnerets black, anteriors and medians yellow. *Legs*: pale yellow with distal black retrolateral streaks on tibiae and additional proximal streaks on tibiae III–IV. Spination of legs I: metatarsi V 4–2–0, P 0–0–1, R 0–0–1; tibiae V 4–2–0, P 0–0–1, R 0–0–1; femora P 0–0–2, D 1–1–1; also on underside of femora I–II a row of paired stiff bristles (also present in ♂, but pale and difficult to see). *Epigyne* (Fig. 15F, G, H): thinly clothed in pale yellowish hairs.

Dimensions (mm): total length 3·2; carapace length 1·45, breadth 1·08, height 0·78; abdomen length 1·76; eyes, AM row 0·68, AL row 0·98, PM row 0·6, PL row 0·67; quadrangle length 0·52. *Ratios*: AM : AL : PM : PL : 9 : 5 : 3·5 : 4; AM : CL : 9 : 3·5.

VARIATION. ♂ from Mali total length 3·28 mm, carapace length 1·4 mm; ♀ total length 2·9–3·2 mm, carapace length 1·36–1·45 mm (3 specimens). In one ♀ from Zaire the median septum and epigynal margins are more pronounced and as such cannot be distinguished from that of *A. stella* (Fig. 16E). Unrubbed ♀'s have a patch of short lanceolate orange setae between the anterior median and posterior median eyes.

DISTRIBUTION. Ghana; Guinea; Mali; Zaire.

MATERIAL EXAMINED. **Ghana**: Accra, Achimota, house, 1♀, v.1961 (*C.P. Hinkley*) (MCZ, Harvard). **Guinea**: Kéoulenta, 1♀, (BMNH). **Mali**: Bamako, holotype ♂, ix.1937 (*L. Berland*) (MNHN, Paris); Fana, 1♂, viii–ix.1971 (*G. Pierrard,* MT. 142.361) (MRAC, Tervuren). **Zaire**: Katanga, Luiswishi 28 km NE Lubumbashi, savannah, 1♂, (*F. Malaisse,* MT. 145.529) (MRAC, Tervuren).

Asemonea stella sp. n.

(Figs 16A–F; 28)

DIAGNOSIS. *A. stella* is closely related to *A. pulchra,* but may be readily distinguished by the black star on the abdomen (Figs 16A; 28) and presence of a distal furrow on the palpal femoral apophysis (Fig. 16C, arrowed). The epigynes cannot be distinguished with certainty.

MALE HOLOTYPE. *Carapace* (Fig. 16A, D): pale yellow grading to whitish yellow in eye region with black v-shaped thoracic marking. *Eyes*: with black surrounds except AM; fringed in silky white hairs. *Clypeus*: pale yellow, shiny; teeth not examined. *Maxillae, labium, sternum and coxae*: pale yellow. *Abdomen*: whitish yellow, shiny, with distinctive black star and two black patches dorsally, underside whitish yellow with black patch in epigynal region; spinnerets black, fringed in dark brown hairs; posteriors elongate with moderately long terminal article; anal tubercle black. *Legs*: legs I pale yellow with black tarsi and black lateral patches on apices of tibiae; legs II–III pale yellow; legs IV pale yellow with black lateral spots at either end of tibiae; spines moderately robust, numerous and pale. Spination of legs I: metatarsi V 2–2–2, P 1–0–1, R 0–0–1; tibiae V 2–4–0, P 0–1–1, R 0–0–1; femora P 0–0–2, D 1–1–1. *Palp* (Fig. 16B, C, F): tegular flange lacking.

Dimensions (mm): total length 3·16; carapace length 1·44, breadth 1·13, height 0·72; abdomen length 1·76; eyes, AM row 0·64, AL row 0.84, PM row 0·54, PL row 0·60; quadrangle length 0·48. *Ratios*: AM : AL : PM : PL : 8 : 4 : 2·6 : 4; AM : CL : 8 : 4.

FEMALE PARATYPE. Similar to ♂ except for the following: *Carapace*: with blackish eye region. *Eyes*: fringed in pale yellow and orange hairs. *Abdomen*: anterior black markings more extensive forming a black patch; spinnerets pale yellow except posteriors which have black terminal articles and black dorsal streaks on basals. *Legs*: legs I–II whitish yellow to pale yellow with distal black retrolateral spots on tibiae; legs III–IV similar, but with additional spots proximally. Spination of legs I: metatarsi V 4–2–0, P 0–0–1; tibiae V 4–2–0, P 0–0–1, R 0–0–1; femora D 1–1–1, P 0–0–2. *Epigyne* (Fig. 16E): vulva not examined, but probably similar to that of *A. pulchra.*

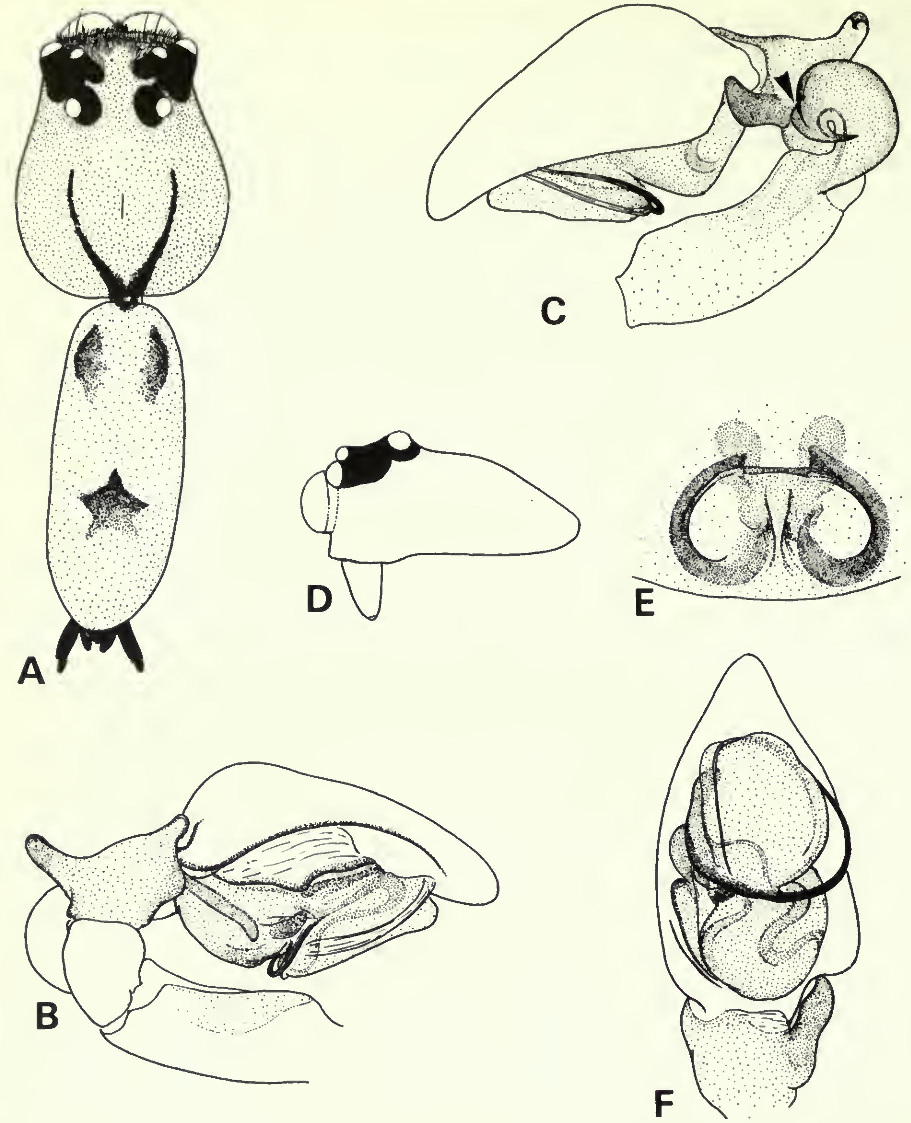

Fig. 16. *Asemonea stella* sp. n., holotype ♂: A, dorsal view; B, palp, ental view; C, palp, ectal view; D, carapace, lateral view; F, palp, ventral view. Paratype ♀: E, epigyne.

Dimensions (mm): total length 3·64; carapace length 1·46, breadth 1·1, height 0·8; abdomen length 2·04; eyes, AM row 0·68, AL row 0·94, PM row 0·6, PL row 0·65; quadrangle length 0·51. Ratios: AM : AL : PM : PL : 8·5 : 4·6 : 3·5 : 4; AM : CL : 8·5 : 4.

VARIATION. ♂ from Kilifi total length 3·16 mm, carapace length 1·28 mm.

DISTRIBUTION. Kenya.

MATERIAL EXAMINED. **Kenya**: Kilifi, garden, holotype ♂, 6.ix.1977 (*J. & F. Murphy*, 6203) (BMNH. 1979.9.28.1); Kilifi, I. Salés, paratype ♀, 9.ix.1977 (*J. & F. Murphy*, 6207); Kilifi, beaten from hedge in open farm land about 200 yds from sea, paratype ♂, 11.viii.1974 (*J. & F. Murphy*, 4038) (BMNH).

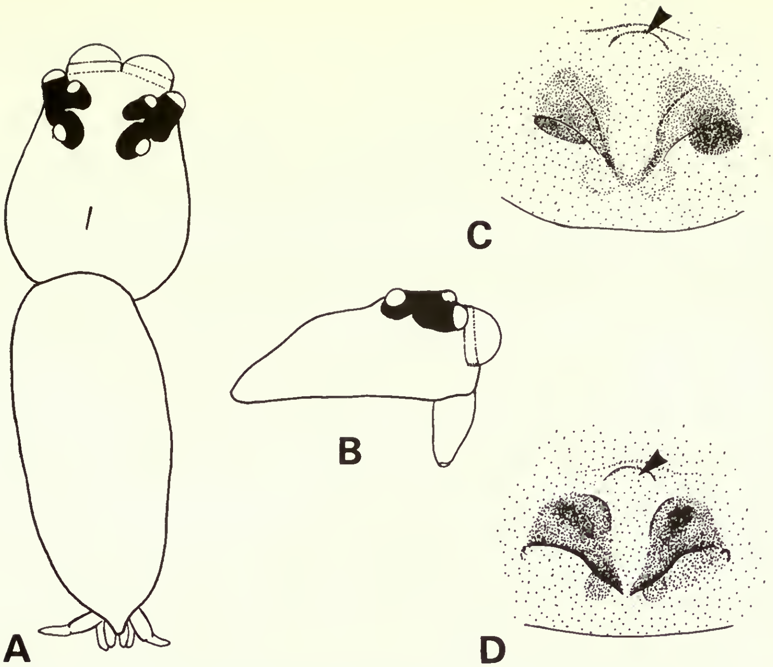

Fig. 17 *Asemonea ornatissima* Peckham, Peckham & Wheeler, lectotype ♀: B, carapace, lateral view; C, epigyne. *A. bella* Lenz, holotype ♀: A, dorsal view; D, epigyne.

Asemonea ornatissima Peckham, Peckham & Wheeler

(Fig. 17A–D)

Asamonea ornatissima Peckham, Peckham & Wheeler, 1888 : 244, ♀. LECTOTYPE ♀ (here designated) Madagascar (MCZ, Harvard) [examined]. Lenz, 1891 : 165. Roewer, 1954 : 927; 1965 : 4.
Asemonea ornatissima: Bonnet, 1955 : 763.
Asanonea bella Lenz, 1891 : 164, ♀. Holotype ♀, Madagascar (ZIZM, Hamburg) [examined]. Bonnet, 1955 : 763. Roewer, 1954 : 927. **Syn. n.**
Asemonea bella: Simon, 1901 : 396.
Asamone bella: Roewer, 1965 : 4 [spelling mistake].

DIAGNOSIS. *A. ornatissima* seems to be most closely related to *A. murphyi,* but may be distinguished by the structure of the epigyne (Fig. 17C, D).

MALE. Unknown.

FEMALE, holotype of *A. bella*. *Carapace* (Fig. 17A): pale amber, lighter in eye region. *Eyes*: with black surrounds except AM; fringed in silky white hairs. *Clypeus*: sparsely clothed in very fine whitish hairs. *Chelicerae*: pale yellow; thinly clothed in fine long hairs; teeth not examined. *Maxillae, labium, sternum and coxae*: pale yellow. *Abdomen*: uniformly pale yellow; spinnerets pale yellow, posteriors elongate with long terminal article. *Legs*: pale yellow; spines strong and numerous, but rather pale. Spination of legs I: metatarsi V 2–2–2, P 1–0–1, R 1–0–1; tibia V 2–4–0, P 0–0–1, R 1–0–1; femora P 0–0–2, D 0–0–2. *Epigyne* (Fig. 17D): anteriorly a shallow depression.

Dimensions (mm): total length 4·48; carapace length about 1·8, breadth 1·52, height 0·88; abdomen length 2·84; eyes, AM row 0·88, AL row 1·18, PM row 0·78, PL row 0·82; quadrangle length 0·64. *Ratios*: AM : AL : PM : PL : 11 : 5·5 : 4 : 5; AM : CL : 11 : 4.

VARIATION. ♀ lectotype of *A. ornatissima,* total length 4·3 mm, carapace (Fig. 17B) length 1·9 mm. The epigyne (Fig. 17C) is evidently plugged in mated females.

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED. **Madagascar**: lectotype ♀ [of *A. ornatissima*] (MCZ, Harvard); Point v. Tamatave, holotype ♀ [of *A. bella*] (ZIZM, Hamburg, 12835).

Asemonea tenuipes O. P.-Cambridge
(Fig. 18A–I)

Lyssomanes (Asemonea) tenuipes O. P.-Cambridge, 1869 : 65, ♂. Holotype ♂, Sri Lanka, (UM, Oxford) [examined]. Savory, 1928 : 165.

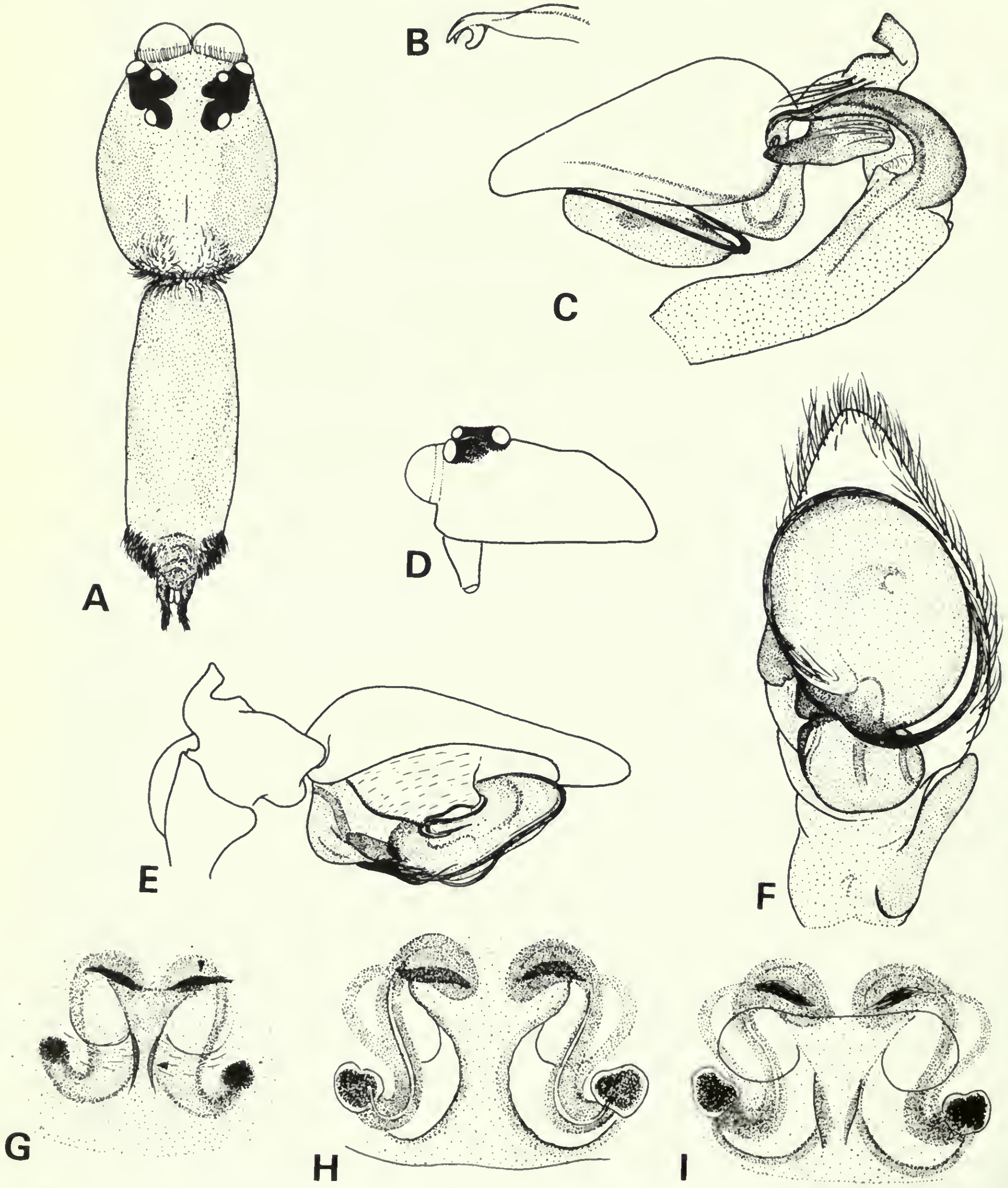

Fig. 18 *Asemonea tenuipes* O. P.-Cambridge, ♂ from Sri Lanka: A, dorsal, view; B, tip of femoral apophysis; C, palp, ectal view; D, carapace, lateral view; E, palp, ental view; F, palp, ventral view. ♀ from Sri Lanka: G, epigyne; H, vulva, dorsal view; I, vulva, ventral view.

Asamonea tenuipes: Simon, 1885 : 27. Peckham, Peckham & Wheeler, 1888 : 242, 243. Peckham & Peckham, 1889 : 31. Roewer, 1954 : 927.

Asemonea tenuipes: Thorell, 1895 : 319. Simon, 1901 : 391–396, 399. Petrunkevitch, 1928 : 181. Sherriffs, 1931 : 537. Bonnet, 1955 : 764; Wanless, 1979 : 185.

Asemonea cingulata Thorell, 1895 : 315, ♂. Holotype ♂, Burma (BMNH) [examined]. Simon, 1901 : 396. Sherriffs, 1931 : 537. Bonnet, 1955 : 763. **Syn. n.**

Asamonea cingulata: Roewer, 1954 : 927.

Lyssomanes andamanensis Tikader, 1977 : 205, ♂, ♀. Holotype ♂, allotype ♀, North Andaman, India (ZSI, Calcutta) [examined]. Tikader, 1978 : 258. **Syn. n.**

Lyssomanes bengalensis Tikader & Biswas, 1978 : 259, ♀. Holotype ♀, West Bengal, India (ZSI, Calcutta) [examined]. **Syn. n.**

DIAGNOSIS. *A. tenuipes* is a distinctive species readily distinguished from all other known species of *Asemonea* by the structure of the palps and epigyne (Fig. 18B, C, E–I).

MALE from Sri Lanka. *Carapace* (Fig. 18A, D): dark amber with eye region and median thoracic area whitish yellow; clothed in dark amber hairs posteriorly. *Eyes*: with black surrounds except AM; AM fringed in pale yellowish hairs, other eyes fringed in very fine weakly iridescent setae. *Clypeus*: clothed in iridescent setae, a black spot in lower vortex between AM. *Chelicerae*: pale amber; thinly clothed in fine light yellowish hairs; promargin with 3 teeth, retromargin with 5. *Maxillae and labium*: pale yellow partly tinged black. *Sternum and coxae*: pale yellow, shiny. *Abdomen*: whitish yellow, lightly tinged black with blackish posterior tip; thinly clothed in minute iridescent setae with tufts of coarse orange-brown hairs anteriorly and on either side of spinnerets; spinnerets whitish yellow tinged black, posteriors grey-black, elongate with curved terminal article. *Legs*: pale yellow with retrolateral stripes on tarsi, metatarsi, tibiae, patellae I–II and apices of femora I–III; spines strong and numerous, pale yellow. Spination of legs I: metatarsi V 2–2–0, P 0–0–1, R 1–0–1; tibiae V 2–4–0, P 0–0–1, R 0–0–1; femora P 0–0–2, D 1–1–1. *Palp* (Fig. 18B, C, E, F): retrolateral femoral apophysis well developed.

Dimensions (mm): total length 4·96; carapace length 1·68, breadth 1·56, height 0·84; abdomen length 2·92; eyes, AM row 0·88, AL row 1·0, PM row 0·62, PL row 0·69; quadrangle length 0·6. *Ratios*: AM : AL : PM : PL : 10·5 : 4·5 : 2·8 : 3; AM : CL : 10·5 : 6·5.

FEMALE from Sri Lanka. *Carapace*: greyish yellow with paler head region. *Eyes*: with black surrounds except AM; fringed in fine silky white hairs. *Clypeus*: clothed in vertically layered silky white hairs that are weakly iridescent under some angles of illumination. *Chelicerae*: pale yellow to whitish, shiny. *Maxillae, labium, sternum and coxae*: more or less as in ♂. *Abdomen*: whitish yellow, fringes lacking. *Legs*: pale yellow with blackish lateral streaks on tarsi and on either end of tibiae IV; spines similar to ♂. Spination of legs I: metatarsi and tibiae V 2–4–0, P 0–0–1, R 0–0–1; femora P 0–0–2, D 1–1–1. *Epigyne* (Fig. 18G–I): openings indistinct.

Dimensions (mm): total length 4·2; carapace length 1·6, breadth 1·16, height 0·78; abdomen length 2·56; eyes, AM row 0·78, AL row 0·92, PM row 0·56, PL row 0·64; quadrangle length 0·52. *Ratios*: AM : AL : PM : PL : 10 : 4 : 3 : 3·4; AM : CL : 10 : 4·5.

VARIATION. ♂ total length 3·84 to 4·96 mm, carapace length 1·64–2·0 mm (9 specimens); ♀ total length 3·76–4·2 mm, carapace length 1·52–1·72 mm (5 specimens).

DISTRIBUTION. Andaman Islands, Burma, India, Sri Lanka, Thailand.

MATERIAL EXAMINED. **Andaman Islands**: Tugapur, Mayabandar, holotype ♂, allotype ♀ [of *L. andamanensis*] 13.v.1971 (*B. K. Tikader*) (ZSI, Calcutta). **Burma**: Tharrawaddy, holotype ♂ [of *A. cingulata*] 1♀, (*E. W. Oates*) (BMNH), Tharrawaddy, 1♀ (*E. W. Oates*) (NR, Stockholm). **India**: West Bengal, Baikunthapur village, Baraipur, Dist., 24, holotype ♀ [of *L. bengalensis*] (*Bijan Biswas*) (ZSI, Calcutta). **Sri Lanka**: holotype ♂ [of *A. tenuipes*] (*G. H. K. Thwaites*) (UM, Oxford); 2♂♂, 1♀, no other data (BMNH); Badulla District, 1♂, 18.viii.1963 (*M. Speight*, Univ. Lond. Ceylon Expd.) (BMNH); 1♂, 1♀, Koch coll, no other data (BMNH); 2♂♂, 2♀♀, no other data (MNHN, Paris). **Thailand**: Bangkok, 1♂, (H. Hillman) (BMNH).

Asemonea cristata Thorell

(Fig. 19A–E)

Asemonea cristata Thorell, 1895 : 316, ♂. Holotype ♂, Burma (BMNH) [examined]. Simon, 1901 : 396. Sherriffs 1931 : 537, 538. Bonnet, 1955 : 763.
Asamonea cristata: Roewer, 1954 : 927.

DIAGNOSIS. *A. cristata* is evidently not closely related to other known species of *Asemonea,* but may be readily separated by the peg-like spines on the palpal tibiae (Fig. 19B, C).

FEMALE. Unknown. Thorell (1895) considered that *A. picta,* described from two females, may belong with this species. This may be correct, but in both specimens of *A. picta* the

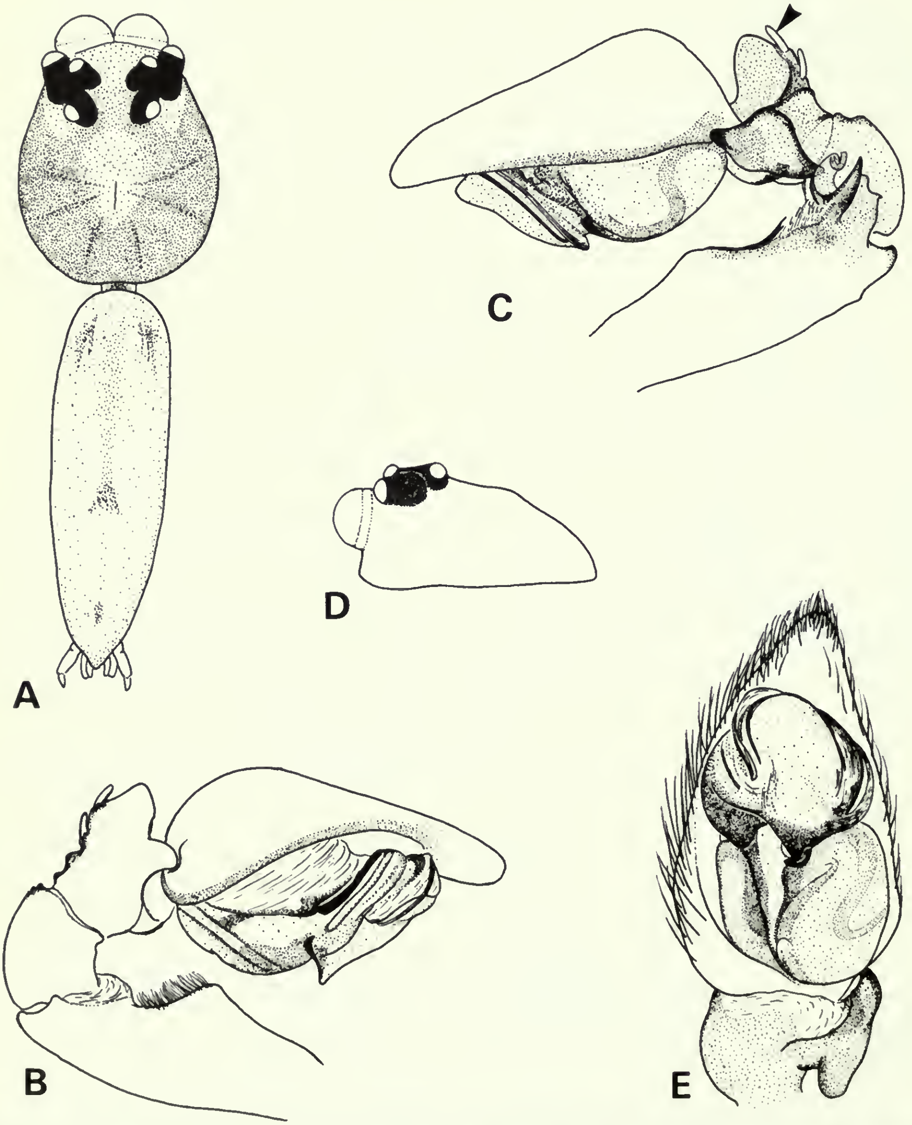

Fig. 19 *Asemonea cristata* Thorell, holotype ♂: A, dorsal view; B, palp, ental view; C, palp, ectal view; D, carapace, lateral view; E, palp, ventral view.

carapace differs in shape from that of *A. cristata*. Although this could be an artifact of preservation it also suggests a degree of sexual dimorphism not previously encountered in *Asemonea*. For the present therefore I propose to regard them as distinct taxa.

Male holotype. *Carapace* (Fig. 19A, D): pale amber grading to whitish yellow in eye and foveal regions. *Eyes*: with black surrounds except AM; sparsely fringed in whitish hairs (?rubbed). *Clypeus*: whitish yellow, (?rubbed). *Chelicerae*: pale yellow; teeth not examined. *Maxillae, labium, sternum and coxae*: pale yellow to whitish yellow, shiny. *Abdomen*: yellow-brown with faint blackish markings; spinnerets yellow-brown faintly tinged black, posteriors elongate with long terminal article. *Legs*: legs I pale yellow with faint black lateral stripes; legs II similar, but stripes lacking on prolateral surface; legs III–IV pale yellow with light brown-black stripes on tibiae and femora; spines strong and numerous, rather pale. Spination of legs I: metatarsi V 4–2–0, P 0–0–1, D 0–1–0, R 1–0–1; tibiae V 4–2–0, P 0–1–2, D 1–1–0, R 0–0–2; femora P 0–0–1, D 1–1–1, R 0–0–1. *Palp* (Fig. 19B, C, E): tegular flange present.

Dimensions (mm): total length 4·4; carapace length 1·76, breadth 1·44, height 0·92; abdomen length 2·6; eyes, AM row 0·84, AL row 1·05, PM row 0·66, PL row 0·71; quadrangle length 0·56. *Ratios*: AM : AL : PM : PL : 10 : 5 : 3·5 : 4; AM : CL : 10 : 6.

Distribution. Burma.

Material examined. **Burma**: Tharrawaddy, holotype ♂ (*E. W. Oates*) (BMNH. 1895. 9.21.957)

Asemonea picta Thorell

(Fig. 20A–C)

Asemonea picta Thorell, 1895 : 318, 2♀♀. LECTOTYPE ♀, (here designated) Burma (BMNH); PARALECTOTYPE ♀, Burma (NR. Stockholm) [examined]. Simon, 1901 : 396. Sherriffs, 1931 : 538; Bonnet, 1955 : 764.
Asamonea picta: Roewer, 1954 : 927.

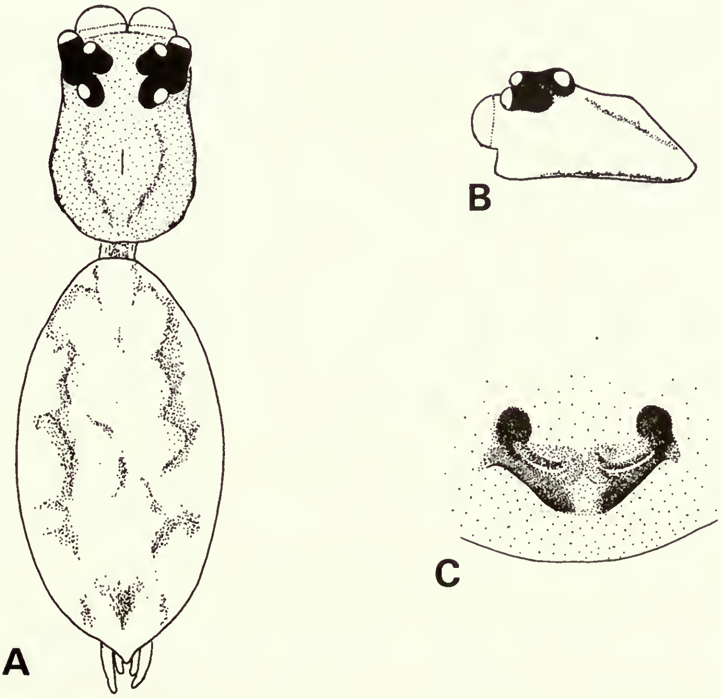

Fig. 20 *Asemonea picta* Thorell, lectotype ♀: A, dorsal view; B, carapace, lateral view; C, epigyne.

DIAGNOSIS. *A. picta* does not appear to be very closely related to other known species of *Asemonea,* from which it can be distinguished by the structure of the epigyne (Fig. 20B).

MALE. Unknown, but possibly conspecific with *A. cristata.*

FEMALE LECTOTYPE. *Carapace* (Fig. 20A, B): pale greyish yellow grading to whitish yellow in eye region with indistinct blackish border line and brownish bands from PL's to near posterior thoracic margin. *Eyes*: with black surrounds except AM; fringed in whitish hairs. *Clypeus*: clothed in fine shining white hairs. *Chelicerae*: pale yellow, shiny; teeth not examined. *Maxillae, labium, sternum and coxae*: whitish yellow. *Abdomen*: whitish yellow with faint greenish brown markings; spinnerets whitish yellow, posteriors elongate with long terminal article. *Legs*: whitish yellow with brownish green spots on either end of tibiae (possibly all that remains of lateral stripes); spines strong and numerous, rather pale. Spination of legs I: metatarsi V 4–2–0, P 0–0–1, R 0–0–1; tibiae V 4–3–2, P 0–1–1, R 0–0–1; femora P 0–0–1, D 1–1–1. *Epigyne* (Fig. 20C): dark red-brown.

Dimensions (mm): total length 4·44; carapace length 1·52, breadth 1·08, height 0·74; abdomen length 2·8; eyes, AM row 0·75, AL row 0·98, PM row 0·61, PL row 0·67; quadrangle length 0·50. *Ratios*: AM : AL : PM : PL : 9·5 : 5 : 3 : 4; AM : CL : 9·5 : 5.

VARIATION. ♀ paralectotype 4·7 mm total length, 1·68 mm carapace length. Although some shrinkage has occurred the shape of the carapace is more or less as in the lectotype.

DISTRIBUTION. Burma.

MATERIAL EXAMINED. **Burma**, Tharrawaddy, Lectotype ♀, (*E. W. Oates*) (BMNH. 1985.9.21.958); paralectotype ♀, same data as lectotype except (NR, Stockholm).

Asemonea pinangensis sp. n.

(Fig. 21A–E)

DIAGNOSIS. *A. pinangensis* is closely related to *A. minuta,* but may be distinguished by the colour markings (Fig. 21A, B), the shape of the palpal femoral apophysis, the lip on the dorsal tibial apophysis (Fig. 21D) and distribution.

FEMALE. Unknown.

MALE HOLOTYPE. *Carapace* (Fig. 21A, B): whitish yellow with heavy black markings; iridescent green under some angles of illumination. *Eyes*: entire region black; sparsely fringed in pale yellowish hairs. *Clypeus*: black with pale yellow band from margin to lower space between AM. *Chelicerae*: whitish yellow with light bluish grey markings, shiny; teeth not examined. *Maxillae, labium, sternum and coxae*: whitish yellow, shiny. *Abdomen*: black with whitish yellow patches; clothed, especially posteriorly, in long grey-black hairs; spinnerets black with grey-black hairs, more or less subequal in length. *Legs*: legs I whitish yellow with black lateral streaks on metatarsi, tibiae, patellae and femora; legs II–III whitish yellow; legs IV whitish yellow with black annuli on femora and both ends of tibiae; spines moderately strong and numerous, pale. Spination of legs I: metatarsi V 4–0–0, P 0–1–1, R 0–1–1; tibiae V 4–2–0, P 0–0–1, R 0–0–1; femora P 0–0–2, D 1–1–1. *Palp* (Fig. 21C, D, E): pale yellowish with heavy black markings.

Dimensions (mm): total length 2·36; carapace, length 1·16, breadth 0·92, height 0·6; abdomen length 1·2; eyes, AM row 0·56, AL row 0·72, PM row 0·46, PL row 0·52; quadrangle length 0·44. *Ratios*: AM : AL : PM : PL : 7 : 3·5 : 2·5 : 3; AM : CL : 7 : 4.

DISTRIBUTION. Malaysia, Pinang Island.

MATERIAL EXAMINED. **Malaysia:** Pinang Island; environs of Telok Bahang, roadside vegetation, net sweeping, holotype ♂, 16.viii. 1979 (*J. & F. Murphy,* 8283) (BMNH. 1979.9.20.2).

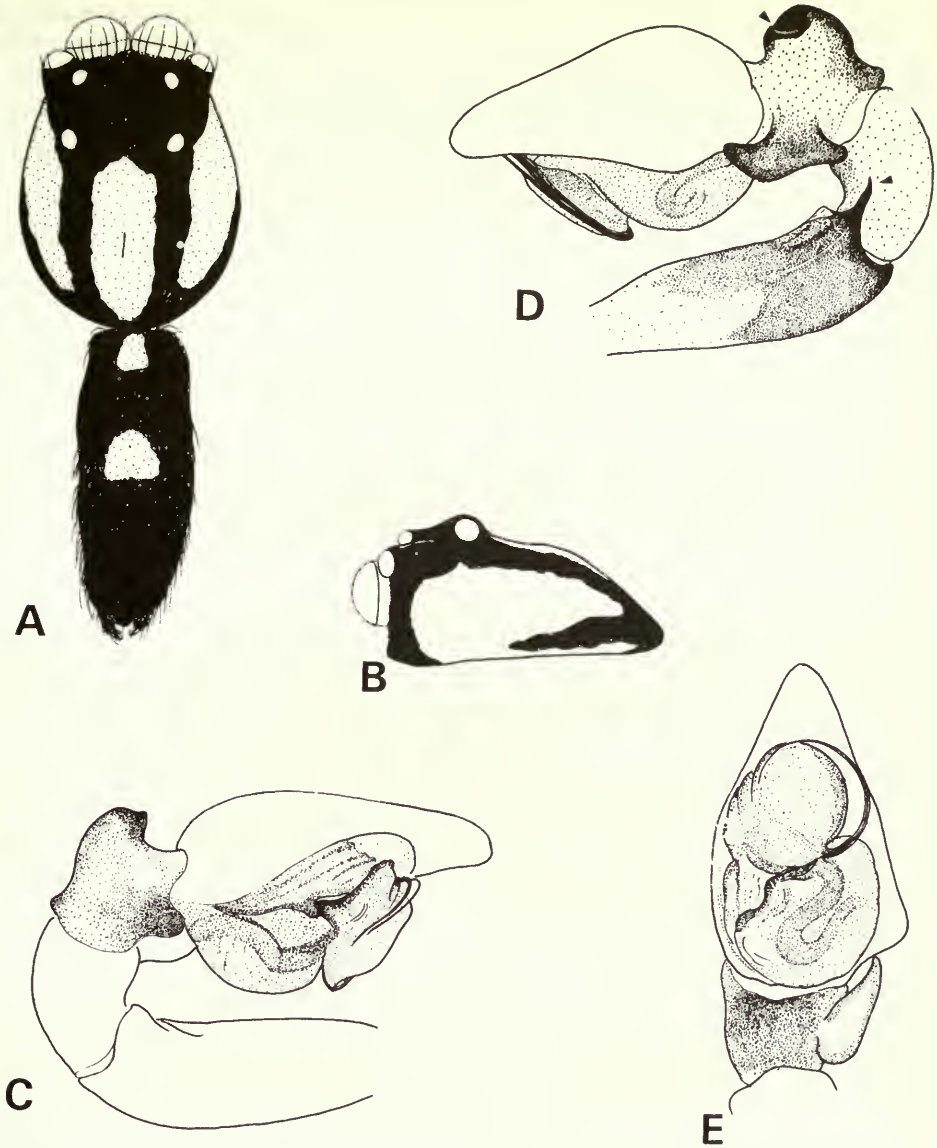

Fig. 21 *Asemonea pinangensis* sp. n., holotype ♂: A, dorsal view; B, carapace, lateral view; C, palp, ental view; D, palp, ectal view; E, palp, ventral view.

Genus *GOLEBA* gen. n.

DEFINITION. Spiders medium in size ranging from about 4·8 to 7·0 mm in length. Sexes alike in general habitus, sexual dimorphism sometimes evident in colour markings; not hirsute. *Carapace*: longer than broad, moderately high with elevated eye region, widest at posterior margin of coxae II; fovea long moderately sulciform, situated more or less midway between posterior lateral eyes and posterior thoracic margin; sculpturing not marked, cuticle sometimes weakly iridescent green. *Eyes*: with black surrounds except anterior medians; set on moderately well developed tubercles; arranged in four transverse rows (rows two and three very close) comprised of anterior medians, anterior laterals, posterior medians and posterior laterals; anterior medians largest, almost occupying full breadth of facies; anterior laterals less than half diameter of anterior medians, positioned behind and plainly wider than first row; posterior medians relatively large, very close to and clearly inside optical axis of anterior laterals; posterior laterals as large or almost as large as anterior laterals, set closer together and well inside lateral margins of carapace; quadrangle formed by posterior median and posterior lateral eyes broader than long; entire quadrangle (measured from base of anterior medians to posterior margin of posterior lateral eyes) occupying between 25 and 30% of carapace length. *Clypeus*: between 50 and 60% of diameter of anterior median eyes; sometimes clothed in fine shining hairs layered perpendicularly, with three curved setae in lower space between anterior median eyes. *Chelicerae*: of medium size, moderately robust, vertical or inclined posteriorly; promargin with three teeth, retromargin with five to seven. *Maxillae*: of medium length, outer margins slightly excavated; convergent. *Labium*: subtriangular, wider than long, about half maxillae length. *Sternum*: cordiform; margins indistinct. *Coxae*: subequal in size. *Abdomen*: elongate; spinnerets unequal in size, posteriors longest, sometimes with long terminal article; anal tubercle a moderately well developed cone; tracheal system not examined. *Legs*: long and slender, spines numerous, long and robust. *Female palps*: long and slender with apical claw. *Secondary genitalia*: complex and inter-specifically distinct; defined under definition of species groups.

TYPE SPECIES: *Asemonea puella* Simon.

DIAGNOSIS. *Goleba* seems on the basis of carapace shape and eye dispositions to be most closely related to *Asemonea*, but may be readily distinguished by the presence of a ventral tubercle on the palpal femora in males (Fig. 22D, 24B) and by the structure of the epigynes in females.

ETYMOLOGY. The generic name is an arbitrary combination of letters.

List of species in the genus *Goleba* gen. n.

Goleba pallens (Blackwall, 1877)
G. puella (Simon, 1885)
G. punctata (Peckham, Peckham & Wheeler, 1888)

REMARKS. Although *Goleba* is only known from three species it may on account of wide differences in genitalic characters be usefully divided into two species groups. The *puella*-group, represented by one species from West and Central Africa and the *pallens*-group with two species from the Malagasy subregion. An identification key is not provided as the species can be readily separated from one another by the genitalia.

The *puella*-group

DEFINITION. The only species known to belong here is characterized by the following secondary genitalic characters. *Male palps* (Fig. 22C, D, E): femora with ventral tubercle; patellae lacking apophyses; tibiae with retrolateral and ventral apophyses; cymbium distally finger-like, fringed in long setae; embolus (e) arising from basal margin of tegulum, proximally stout (possibly as a result of fusion between the embolic guide and embolus) distally long and thread-like; tegulum (t) elongate, irregular in outline with sinuous ducts, on apical dorsal surface a flange (f) which may, in the resting palp, protect the embolic tip; subtegulum (st) bulbus with sinuous ducts, an anterior lobe (l) and apophysis (m). The lobe-like structure (x) arises from the basal haematodocha and seems to form part of the locking mechanism which keeps the tegulum and subtegulum in position. *Epigyne*: with anteriorly situated atrium and median posterior scape; introductory ducts indistinct; spermathecae large evidently lobed and associated with well developed gland-like tubules.

Goleba puella (Simon) comb. n.

(Figs 22A–E; 23A–C; 29)

Asamonea puella Simon, 1885 : 27, ♂, ♀. LECTOTYPE ♂, 3♀♀ PARALECTOTYPES (here designated)

Angola (MNHN, Paris) [examined]. Peckham & Peckham & Wheeler, 1888 : 242. Peckham & Peckham, 1889 : 31. Roewer, 1954 : 927; 1965 : 4.
Asemonea puella: Bonnet, 1955 : 764. Clark, 1974 : 12.

Diagnosis. *G. puella* is evidently not closely related to other known species in the genus, but may be distinguished by the absence of a conductor in males and presence of an epigynal scape in females (Figs 22C–E; 23A–C).

Male from Angola. *Carapace* (Fig. 22A, D): pale amber, yellowish in eye region with indistinct sooty bands marginally and extending from PL's to posterior thoracic margin; weakly iridescent under some angles of illumination. *Eyes*: with black surrounds except AM; fringed in shining whitish hairs. *Clypeus*: clothed in fine shining hairs. *Chelicerae*: pale yellow with sooty transverse basal bands, shiny; promargin with 3 teeth, retromargin with 5.

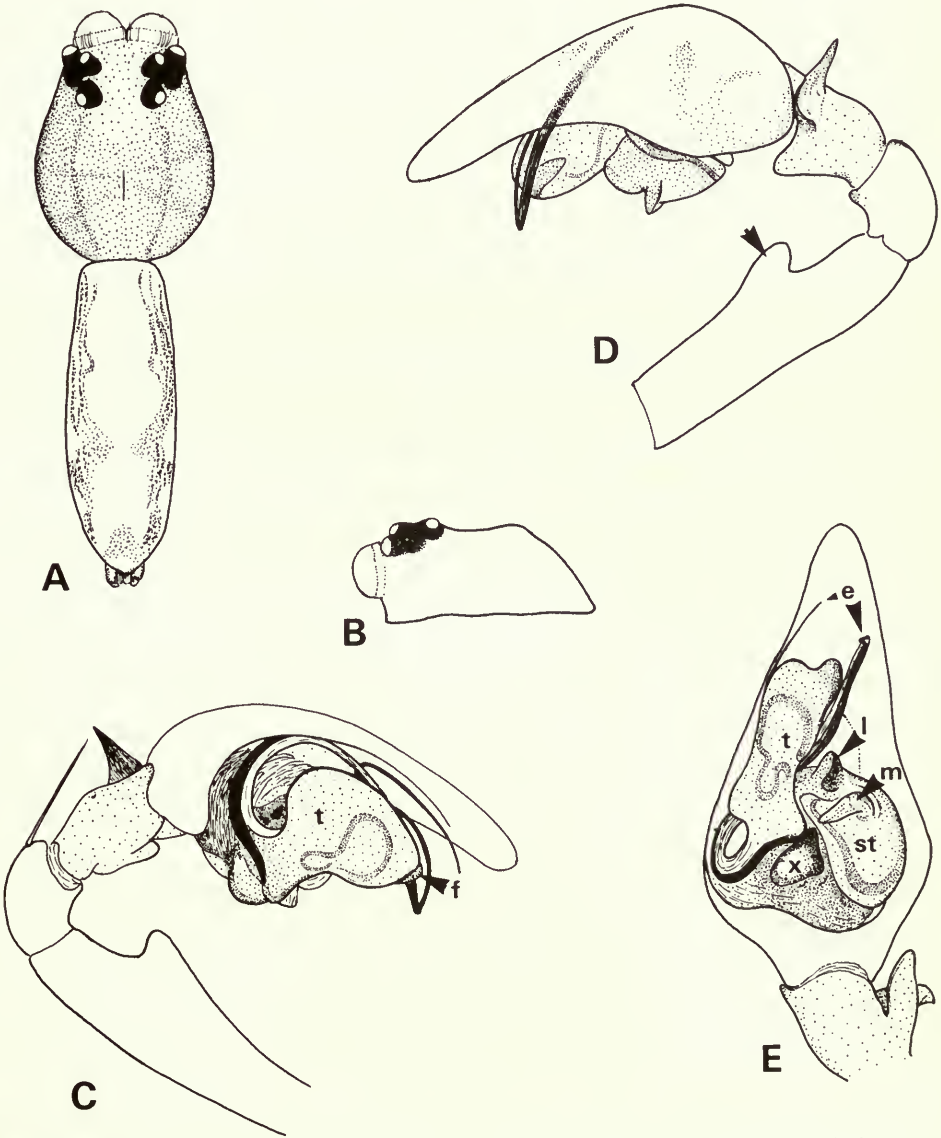

Fig. 22 *Goleba puella* (Simon), ♂ from Angola: A, dorsal view; B, carapace, lateral view; C, palp, ental view; D, palp, ectal view; E, palp, ventral view.

Maxillae and labium: pale yellow. *Sternum*: whitish yellow. *Coxae*: pale yellow. *Abdomen*: whitish yellow with blackish markings; spinnerets whitish yellow, posteriors lightly tinged black and only slightly longer than anteriors and medians. *Legs*: pale yellow grading to amber distally with vague black lateral stripes on legs I and indistinct sooty annuli on femora III–IV; spines strong and numerous. Spination of legs I: metatarsi V 2–4–0, P 1–0–1, R 1–0–1, D 0–1–0; tibiae V 2–2–2, P 1–0–1, D 1–1–0, R 0–1–1; patellae P 0–1–0, R 0–1–0; femora P 0–0–2, D 1–1–2, R 1–1–0. *Palps* (Fig. 22B, C, E): apophysis (m) although elongate is considered to be homologus with the apophysis found in *G. pallens* and *Pandisus.*

Dimensions (mm): total length 5·2; carapace length 2·16, breadth 1·76, height 0·96; abdomen length 3·0; eyes, AM row 1·02, AL row 1·22, PM row 0·84, PL row 0·87; quadrangle length 0·64. *Ratios*: AM : AL : PM : PL : 12·5 : 5 : 3·5 : 4; AM : CL : 12·5 : 7.

FEMALE from Ghana. Similar to ♂ except for the following: *Carapace*: lacking marginal and thoracic markings. *Chelicerae*: without black basal bands: promargin with 3 teeth, retromargin with 7. *Abdomen*: whitish yellow. *Legs*: pale yellow. Spination of legs I: metatarsi V 2–4–0, P 1–0–1, R 1–0–1; tibiae V 2–2–2, P 0–1–1, R 0–1–1; femora P 0–0–2, D 1–1–2, R 0–1–0. *Epigyne* (Fig. 23A–C): openings indistinct; gland-like tubules well developed and visible through the integument.

Dimensions (mm): total length 4·88; carapace length 2·04, breadth 1·56, height 0·92; abdomen length 3·16; eyes, AM row 0·96, AL row 1·14, PM row 0·76, PL row 0·8; quadrangle length 0·60. *Ratios*: AM : AL : PM : PL : 12 : 4·6 : 3 : 4; AM : CL : 12 : 6.

VARIATION. ♂ total length 5·0 to 5·2 mm, carapace length 2·08–2·16 mm (3 specimens); ♀ total length 4·8–6·04 mm, carapace length 2·04–2·28 mm (5 specimens).

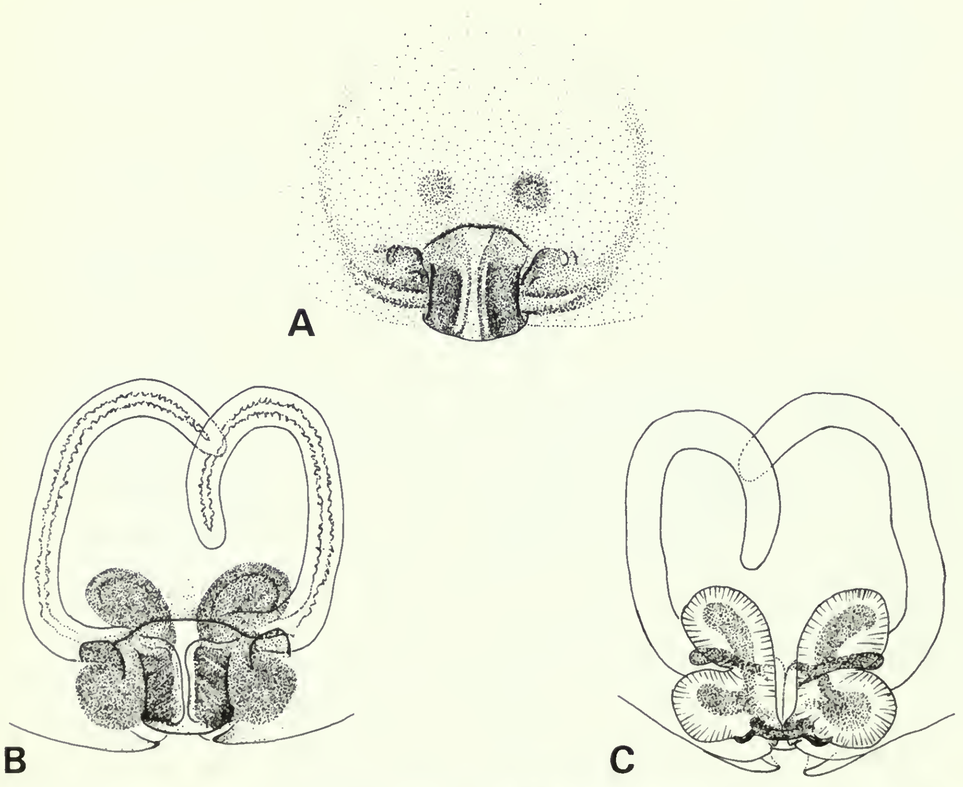

Fig. 23 *Goleba puella* (Simon), ♀ from Ghana: A, epigyne; B, vulva, ventral view; C, vulva, dorsal view.

DISTRIBUTION. Angola; Ghana; Kenya; Zaire.

MATERIAL EXAMINED. **Angola**: Cabinda, Landana, lectotype ♂, 3♀♀ paralectotypes, (*Petit*) (MNHN, Paris, 6812); N'Dalla Tondo, 1♂, 1♀, 26.xi.1908 (*Ansorge*) (BMNH); Dundo, 1♂, 1969 (*A. de Barros Machado,* Ang. 22430). **Ghana**: Accra, Achimota, in garden, 1♀, v.1961 (*C.P. Hinckley*) (MCZ, Harvard); Takoradi, 1♀, 6.i.1960 (*M.B. Usher*) (BMNH). **Kenya**: Kilifi, taken from living green leaves growing low down on trunk of a sausage tree *Kigelia africana*, 1♀, 11.viii.1974 (*J. & F. Murphy*, 4339). **Zaire**: Abimva, 1♀, vi.1925 (*H. Schouteden,* MT. 31276) (MRAC, Tervuren).

The *pallens*-group

DEFINITION. This group is comprised of two species, *G. pallens* from the Seychelles and Aldabra and *G. punctata* from Madagascar. The secondary genitalia are distinctive and confusion with the *puella*-group is unlikely. Unfortunately only the male of *G. pallens* is known.

Male palps: femora and patellae more or less as in the *puella*-group; tibiae with retrolateral and dorsal apophyses; cymbium distally finger-like, fringed in long setae; embolus (e) originating below tegulum (i.e. in ventral view), long and thread-like, retained in heavily sclerotized conductor (c) which terminates distally in a spur (s); tegulum (t) irregular in outline; subtegulum (st) bulbus with anterior lobe (al), sinuous ducts and scale-like apophysis (m) (probably homologous with that found in *G. puella* and *Pandisus*). *Epigynes*: opening indistinct; scape lacking; ducts wide and convoluted; spermathecae relatively large; gland-like tubules apparently absent.

Goleba pallens (Blackwall) comb. n.

(Fig. 24A–H)

Lyssomanes pallens Blackwall, 1877; subadult ♂. Holotype subadult ♂, Seychelles (UM, Oxford) [examined]. Peckham, Peckham & Wheeler, 1888 : 246.

Asemonea pallens: Simon, 1901 : 396. Hirst, 1911 : 382. Bonnet, 1955 : 763. Wanless (in press *a*).

Asamonea pallens: Roewer, 1954 : 927.

DIAGNOSIS. *G. pallens* is most closely related to *G. punctata* from which it may be separated by the posterior epigynal openings (Fig. 24F).

MALE (formerly undescribed) from Aldabra. *Carapace* (Fig. 24A, C): pale amber grading to whitish yellow in eye region, shiny. *Eyes*: with black surrounds except AM; fringed in shining silky white hairs. *Clypeus*: with transverse band of light orange hairs. *Chelicerae*: pale yellow, shiny; teeth not examined. *Maxillae and labium*: pale yellow. *Sternum*: whitish yellow. *Coxae*: pale yellow. *Abdomen*: whitish yellow with poorly defined longitudinal reddish brown bands; spinnerets pale yellow: posteriors with long terminal article. *Legs*: light yellow grading to pale amber distally with obscure dark amber stripes on retrolateral surface of tibiae I–II; spines strong and numerous. Spination of legs I: metatarsi V 2–2–0, P 1–0–1, R 0–0–1, D 0–1–0; tibiae V 2–2–2, P 0–1–1, R 0–1–1, D 1–1–0; patellae P 0–1–0, R 0–1–0; femora P 0–1–1, D 1–1–1, R 1–1–1. *Palp* (Fig. 24B, D, E): embolus long and slender, retained for much of its length in the heavily sclerotized conductor.

Dimensions (mm): total length 4·4; carapace length 1·8, breadth 1·48, height 0·8; abdomen length 2·56; eyes, AM row 0·86, AL row 0·96, PM row 0·64, PL row 0·68; quadrangle length 0·51. *Ratios*: AM : AL : PM : PL : 10·5 : 3·8 : 2·5 : 3·5 : AM : CL : 10·5 : 6.

FEMALE from Aldabra. Similar to ♂ except for the following: *Clypeus*: clothed in shining silky white hairs. *Abdomen*: dorsal markings evidently lacking. *Legs*: pale yellow. Spination of legs I: metatarsi V 4–0–0, P 1–1–1, R 1–1–1; tibiae V 4–2–0, P 1–1–0, R 0–1–1; patellae R 0–1–0; femora P 0–0–2, D 1–1–1, R 0–0–1. *Epigyne* (Fig. 24F–H): ducts broad and convoluted.

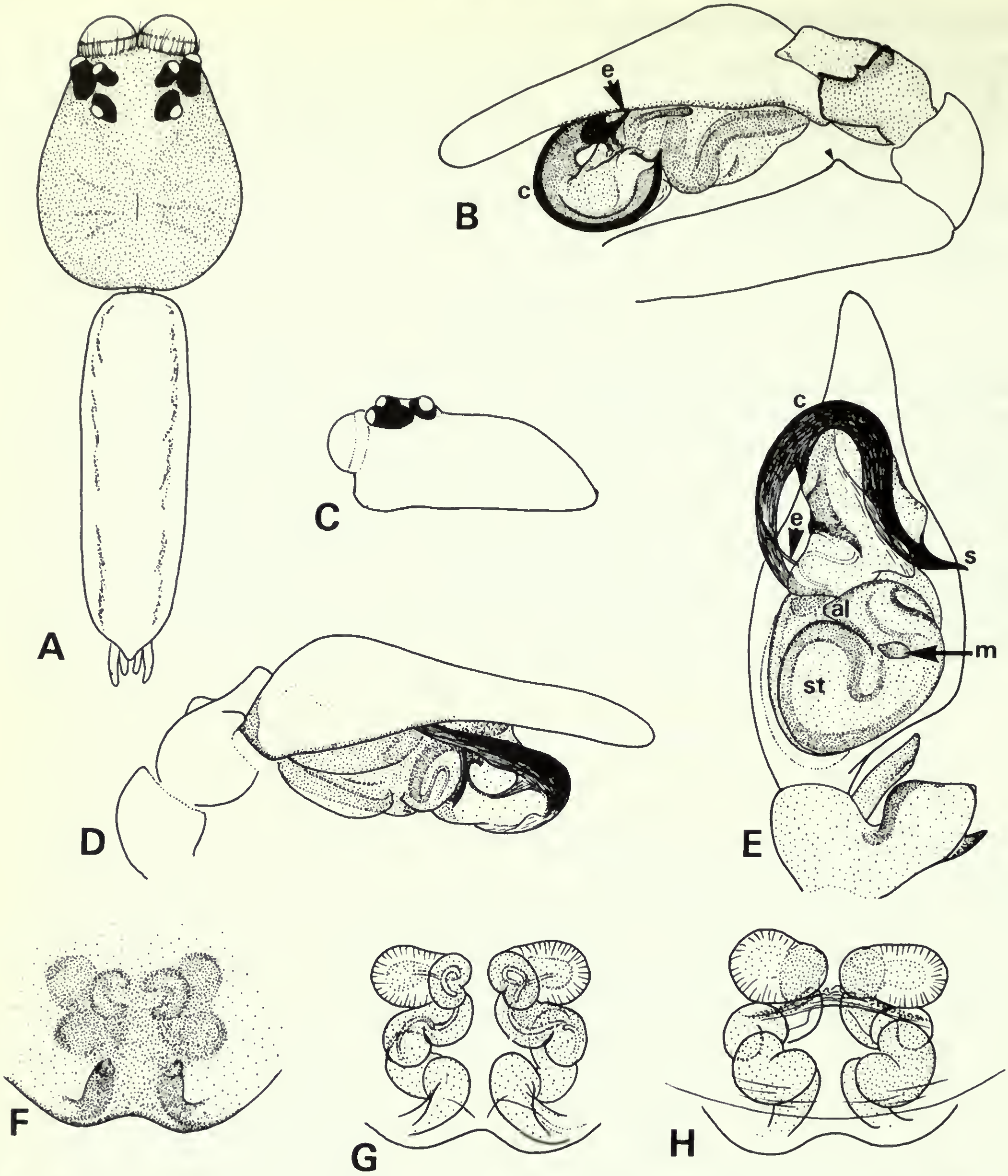

Fig. 24 *Goleba pallens* (Blackwall), ♂ from Aldabra: A, dorsal view; B, palp, ectal view; C, carapace, lateral view; D, palp, ental view; E, palp, ventral view. ♀ from Aldabra: F, epigyne; G, vulva, dorsal view; H, vulva, ventral view.

Dimensions (mm): total length 4·76; carapace length 1·92, breadth 1·4, height 0·84; abdomen length 2·72; eyes, AM row 0·88, AL row 0·96, PM row 0·64, PL row 0·68; quadrangle length 0·51. *Ratios*: AM : AL : PM : PL : 11 : 4 : 2·6 : 3·6; AM : CL : 11 : 6.

VARIATION. ♀ total length 4·5 to 5·3 mm, carapace length 1·92–2·24 mm (3 specimens).

DISTRIBUTION. Aldabra Atoll; Seychelles.

MATERIAL EXAMINED. **Aldabra Atoll**: South Island, Takamaka Grove, 1♂, 1♀, 1–17.ii.1968 (*B. Cogan & A. Hutson,* Royal Society Exp., 1967–8) (BMNH) **Seychelles:** holotype subadult ♂, (*E. Perceval Wright*) (UM, Oxford); Denis Island, 1♀, (*J.S. Gardener*) (BMNH); Silhouette Island, 1♀, (Percy Sladen Trust Exp., 1905) (BMNH).

Goleba punctata (Peckham, Peckham & Wheeler) comb. n.

(Fig. 25A–F)

Asamonea punctata Peckham, Peckham & Wheeler, 1888 : 244, ♀ and immature ♂. LECTOTYPE ♀ (here designated) Madagascar (MCZ, Harvard) [examined]. Roewer, 1954 : 927; 1965 : 4.
Asemonea punctata: Simon, 1901 : 396. Bonnet, 1955 : 764.

DIAGNOSIS. *G. punctata* is most closely related to *G. pallens,* but may be distinguished by the median epigynal openings (Fig. 25C).

MALE. Unknown.

FEMALE from Mahasoa. *Carapace* (Fig. 25A, B): pale yellow-brown with broken dark reddish brown bands from PL's to posterior thoracic margin. *Eyes*: with black surrounds except AM; fringed in silky white hairs. *Clypeus*: clothed in fine shining white hairs. *Chelicerae*: yellow-brown; promargin with 3 teeth, retromargin with 7. *Maxillae, labium, sternum and coxae*: pale yellow. *Abdomen*: whitish yellow with purple-black stripes anteriorly and spots posteriorly; clothed in very fine light yellowish hairs; spinnerets whitish yellow; posteriors with long terminal article. *Legs*: pale yellow; spines strong and numerous, rather pale. Spination of legs I: metatarsi V 4–2–0, P 0–0–1, R 0–0–1; tibiae V 2–2–2, P 1–0–1, R 1–0–1; patellae P 0–1–0, R 0–1–0; femora P 0–1–1, D 1–1–1, R 1–1–1. *Epigyne* (Fig. 25C–F): varies with view point.

Dimensions (mm): total length 6·9; carapace length 2·88, breadth 2·28 height 1·12; abdomen length 4·0; eyes, AM row 1·46, AL row 1·36, PM row 0·95, PL row 1·0; quadrangle length 0·72. *Ratios*: AM : AL : PM : PL : 15 : 5 : 4 : 5; AM : CL : 15 : 9.

VARIATION. ♀ total length 6·6 to 6·9 mm, carapace length 2·64–2·88 mm (4 specimens). The carapace markings are sometimes lost in preserved specimens. The epigyne is somewhat translucent and its appearance alters with view point. In one specimen the openings were plugged.

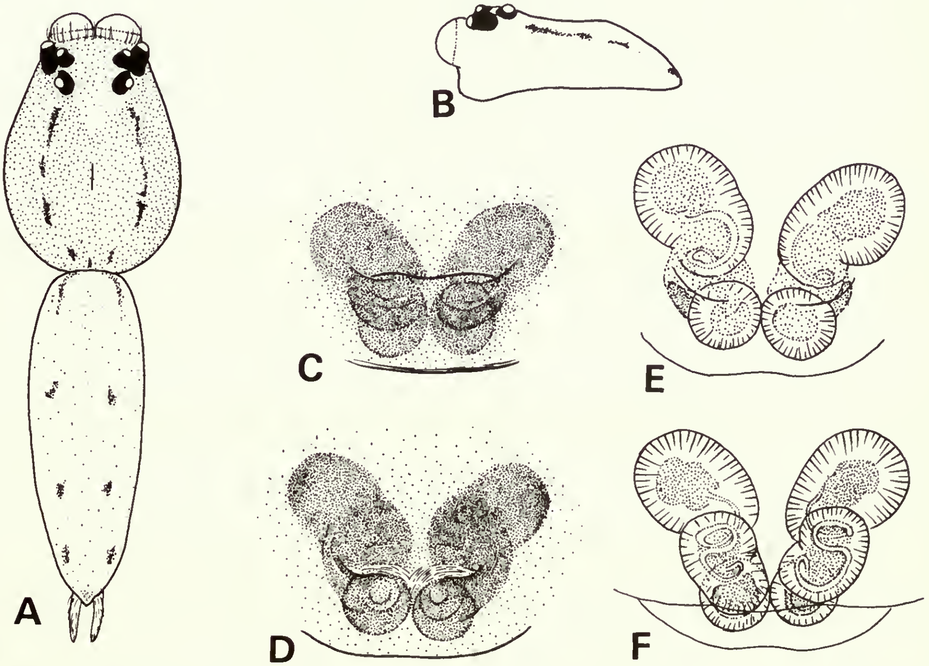

Fig. 25 *Goleba punctata* (Peckham, Peckham & Wheeler), ♀ from Mahasoa: A, dorsal view; B, carapace, lateral view; C, epigyne, ventral view; D, epigyne, viewed slightly from behind; E, vulva, ventral view; F, vulva, dorsal view.

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED. **Madagascar**: lectotype ♀, (MCZ, Harvard); Massif Andringitra, Mahasoa, 2100 m, 1♀, x.1971 (*B. Ranson,* MT. 142.844); Beanana, 1♀, ii.1970 (*A. Lambillon,* MT. 142.671) (MRAC, Tervuren); Antongil, 1♀, (*A. Mocqueries*) (MNHN, Paris, 20202).

Species inquirenda

Lyssomanes sikkimensis Tikader

Lyssomanes sikkimensis Tikader, 1967 : 120, ♀. Holotype ♀, Ligship, West Sikkim, India. Tikader, 1977 : 206.

I have not examined the type of this species, but to judge from the original description (Tikader, 1967) it cannot be placed in any Lyssomaninae genera. The single tooth on the inner cheliceral margin indicates that it belongs somewhere in the unidentati (Simon, 1901).

Acknowledgements

I am grateful to Mr & Mrs John Murphy, London for allowing me to study their collections of African and Malaysian salticid spiders. Mrs Frances Murphy kindly supplied the photographs for figures 26–29 and allowed me to include her observations on the behaviour of *A. murphyi.*

Colleagues kindly made types and other material available for study: Professor P. L. G. Benoit, Musée Royal d'Afrique Centrale, Tervuren, Belgian (MRAC, Tervuren); Mr M. W. R. de V. Graham, The University Museum, Oxford (UM, Oxford); M. M. Hubert, Muséum National d'Histoire Naturelle, Paris, France (MNHN, Paris); Professor T. Kronestedt, Naturhistoriska Riksmuseet, Stockholm, Sweden (NR, Stockholm); Professor H. W. Levi, Museum of Comparative Zoology, Harvard, U.S.A. (MCZ, Harvard); Professor A. de Barros Machado, Lisbon; Dr G. Rack, Zoologisches Institut und Zoologisches Museum, Hamburg (ZIZM, Hamburg); Dr B. K. Tikader, Zoological Survey of India, Calcutta (ZSI, Calcutta).

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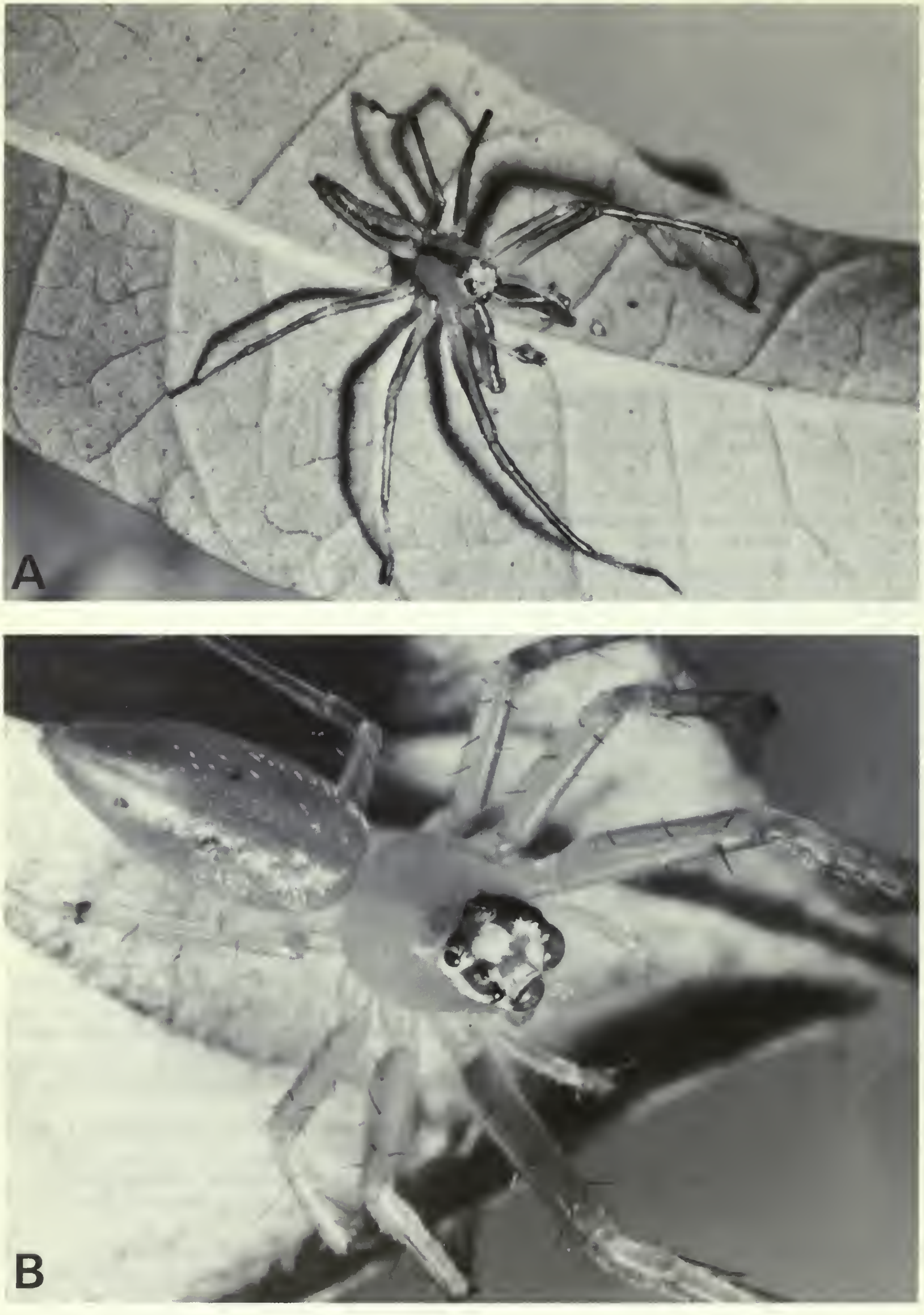

Fig. 26 *Lyssomanes viridis* (Walckenaer): A, ♂; B, ♀.

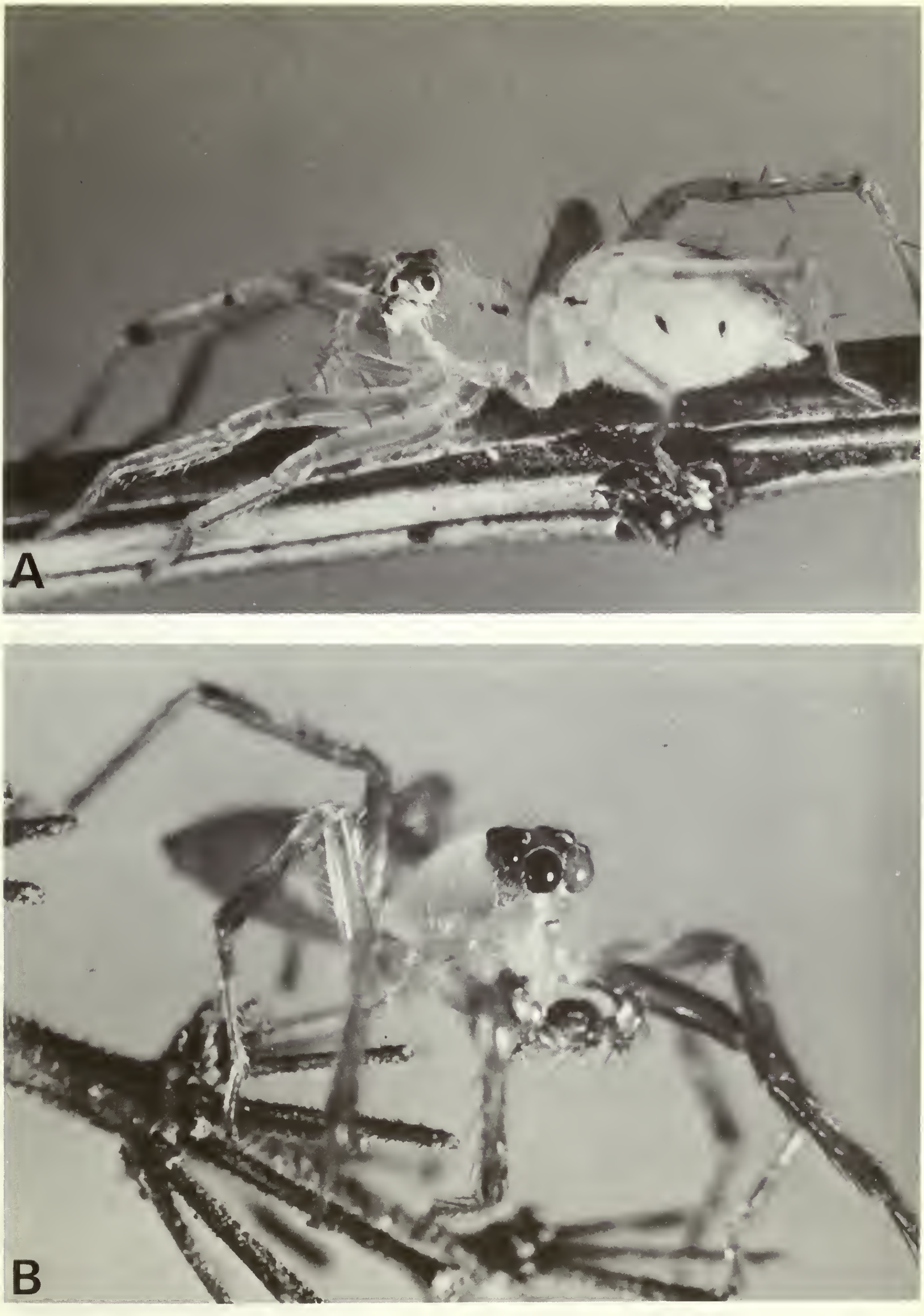

Fig. 27 *Asemonea murphyi* sp. n.: A, ♀; B, ♂.

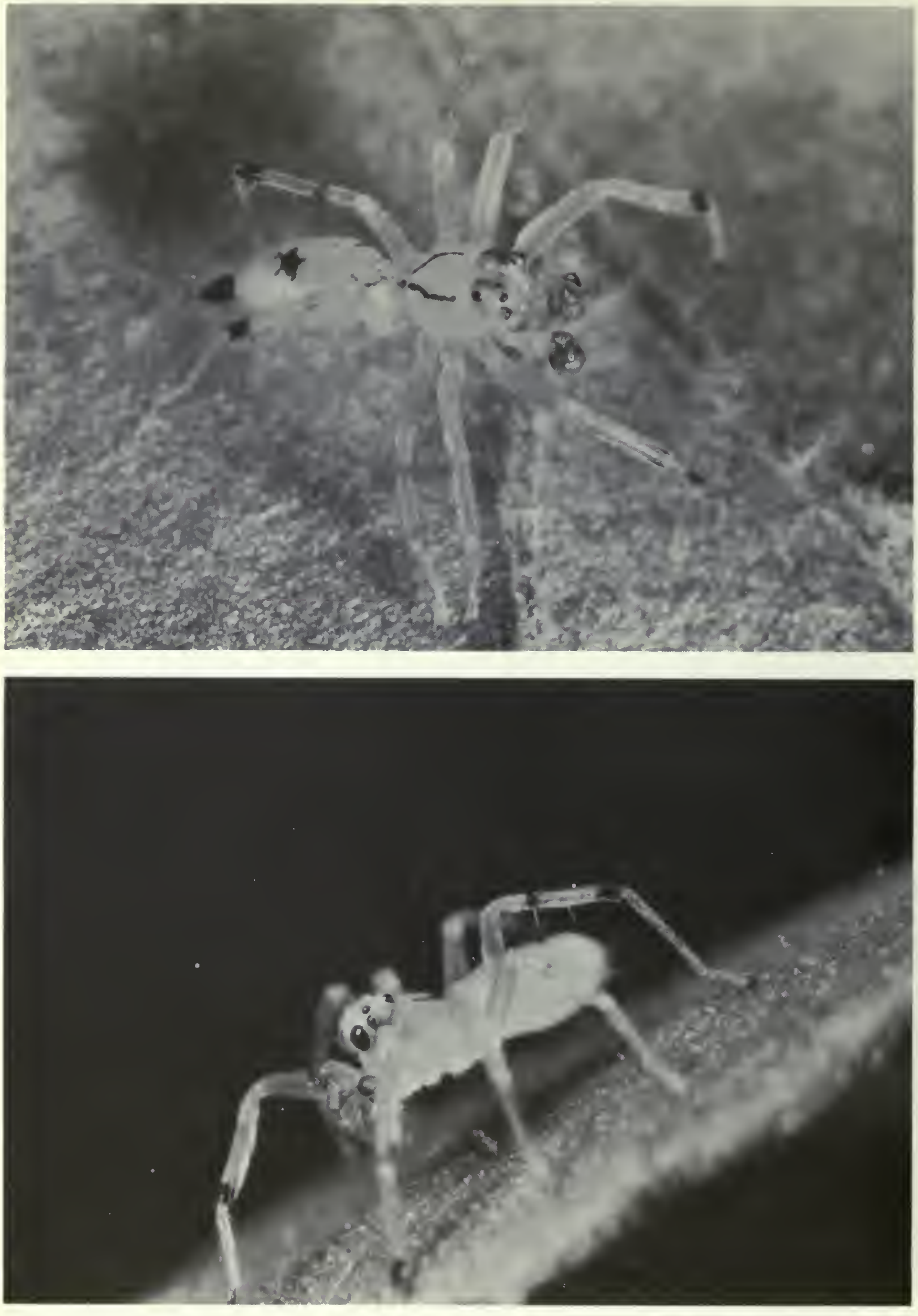

Fig. 28 *Asemonea stella* sp. n., ♂♂.

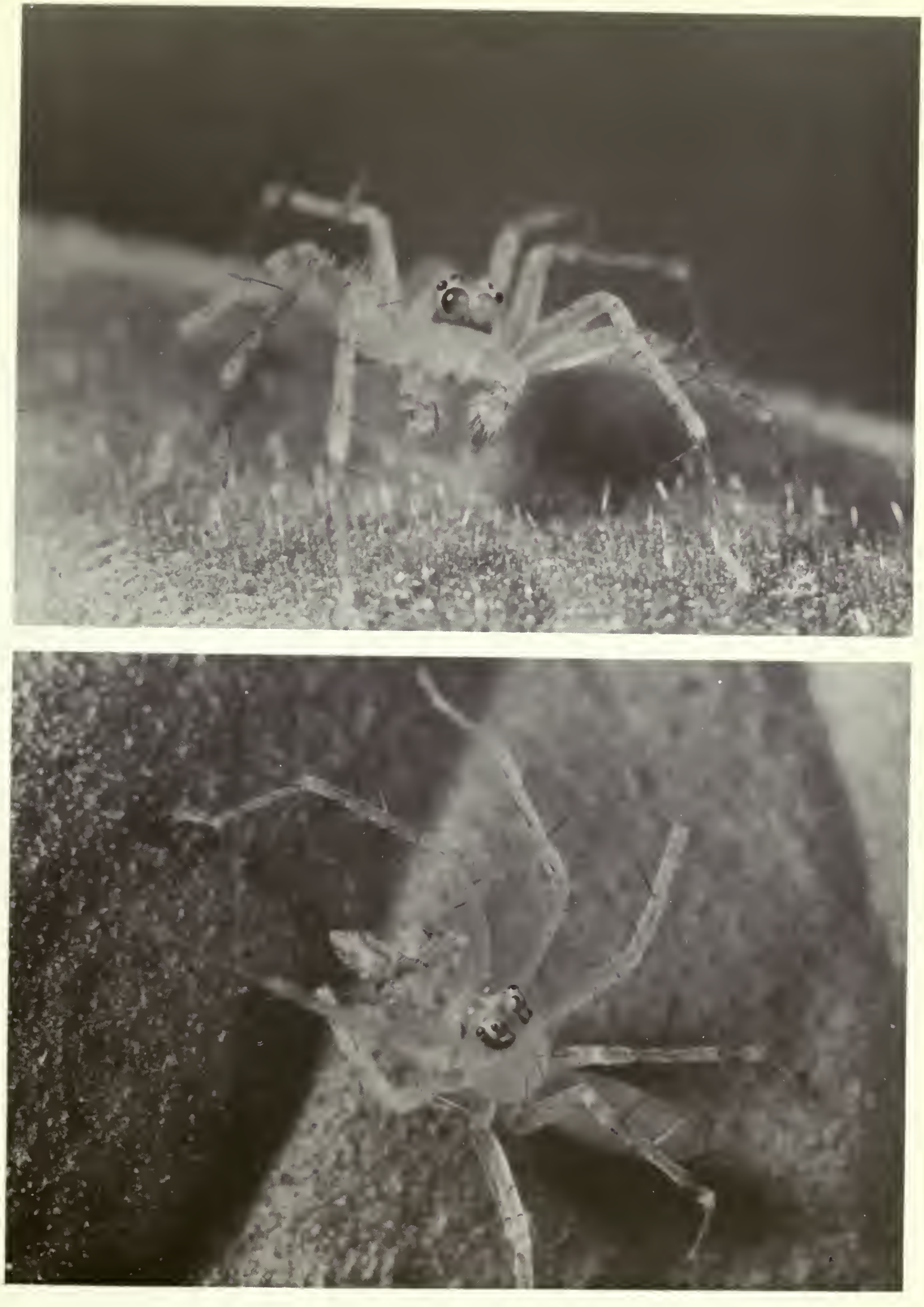

Fig. 29 *Goleba puella* (Simon), ♂♂.

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Contents

A revision of *Reophax* and its type-species, with remarks on several other Recent hormosinid species (Protozoa: Foraminiferida) in the Collections of the British Museum (Natural History). By P. Brönnimann & J. E. Whittaker 259

The coelenterate taxa of Joshua Alder. By P. F. S. Cornelius & J. B. Garfath . . 273

The new genus of toad (Anura: Bufonidae) from the Republic of South Africa with remarks on its relationships. By A. G. C. Grandison 293

Aspects of breeding morphology in *Mertensophryne micranotis* (Anura: Bufonidae): secondary sexual characters, eggs and tadpole. By A. G. C. Grandison 299

A new species of *Crocidura* from Nigeria. By R. Hutterer & P. D. Jenkins . . 305

A revision of *Reophax* and its type-species, with remarks on several other Recent hormosinid species (Protozoa: Foraminiferida) in the Collections of the British Museum (Natural History)

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I. The genus *Reophax* de Montfort, and its type species *R. scorpiurus* de Montfort

(a) The taxonomic status of the genus *Reophax* de Montfort

De Montfort (1808 : 331) introduced the genus *Reophax* ('Réophage; en latin, Reophax') as the 83rd genus of his conchiological system of classification, with the type-species, *Reophax scorpiurus* de Montfort ('Le Réophage queue de scorpion'). It was designated apparently on the basis of a single specimen illustrated by Soldani (1795 : pl. 162, fig. K), one of his 'corpuscula maris dubia et incerta', contained in 'vas 319' from the Mediterranean. Soldani (*op. cit.* : 239) had written of figs I and K of pl. 162 . . . 'Quae supersunt reliqua I, & K mihi ignota prorsus sunt, nisi fortasse K ad Orthoceratis speciem aliquam pertineat . . .', and it is clear that he was unable, at the time, to place either specimen within his system, hence they are described under the heading (p. 209): 'Classis Tertia. Sistens Testacea Bivalvia, Frumentaria, Dubia ac Zoophyta. Cui additur Supplementum Analysim continens marini sedimenti'.

The genus *Reophax* is defined by de Montfort (1808 : 331) as . . . 'Coquille libre, univalve, cloisonnée; droite, sinuée et insectée, ou offrant plusieurs étranglemens, les concamérations augmentant de volume avec l'âge; bouche terminale, arrondie; siphon central'. On the same page de Montfort continues with a description of the type-species which he illustrates on the opposite page (p. 330) with a copy in rather stylized form (and upside-down) of Soldani's original figure. He writes . . . 'Rangé parmi les coquilles droites, il est cependant un peu sinueux, mais point tors. Ses chambres sont séparées les unes des autres par autant d'étranglemens qui rappellent ceux des insectes, en donnant à leur ensemble l'aspect de la queue d'un scorpion. Elles deviennent successivement plus grandes, singulièrement quadrillées, et on ne peut mieux les comparer qu'à autant de petites lanternes hexagones, enfilées les unes aux autres. Elles sont toutes traversées par un siphon qui leur est commun, et qui partant de la base où il sert de bouche, va se rendre au sommet'.

At first sight it seems that de Montfort possessed no material of *R. scorpiurus* of his own as he writes (*loc. cit.* : 332) . . . 'C'est sur la confiance que nous inspire Soldani que nous avons publié cette coquille cloisonnée, qui se trouve dans les sables de la mer Adriatique; ce savant laborieux, doué d'une patience extraordinaire, avoit réuni dans de petits vases des millions de coquilles microscopiques qu'il décrivoit; il avoit su trier et séparer chaque espèce, et dès-lors au milieu de tant de points de comparaison, on ne peut lui contester les formes qu'il publia'. However, in the next paragraph he adds a remark on the colour of the test . . . 'Lorsque le réophage queue de scorpion est encore frais dans ses teintes, il présente celles

Bull. Br. Mus. nat. Hist. (Zool.) **39** (5) : 259–272

Issued 18 December 1980

orangées; exposé au soleil il se décolore, et d'autrefois il prend un ton ocracé. Il a quelquefois une demi-ligne de longueur', an observation which does not occur in Soldani's work, and may be taken to imply that de Montfort had his own collection. In an attempt to shed light on this possibility, one of us (P. B.) wrote to Mme Y. LeCalvez in Paris, inquiring of the whereabouts of a 'De Montfort Collection', and in particular *R. scorpiurus*. She replied (letter dated 21 : 6 : 77) that it is not in the Museum of Natural History, Paris, nor does anyone seem to know what has happened to it and therefore must be presumed lost. This fate must also be assumed for Soldani's collection.

De Montfort's description of *Reophax* and its type-species conform to the International Code of Zoological Nomenclature and are taxonomically valid. Nevertheless, much is missing from the original definition or is of a confusing nature. Nothing is said, for instance, about the constitution of the wall in *R. scorpiurus*, an omission which may either reflect the fact that de Montfort had not examined specimens at first hand, or, as is more likely, was because the taxonomic significance of wall texture was not at that time recognized. An uncertainty also exists concerning the 'siphon central' which is said to be common to, and to traverse all the chambers. If this is not just a generalization, it could indicate a condition found in *Ginesina* Bermúdez & Key, a subglobular-chambered genus in which the apertural necks are rather long and, if preserved in succeeding chambers, give the impression of a continuous siphon. *Ginesina* was placed in synonymy with *Reophax* by Loeblich & Tappan (1964 : 216). The form and position of the aperture of *R. scorpiurus*, on the other hand, were clearly defined by de Montfort as rounded and terminal; nothing was said about the presence or absence of a neck.

Parker & Jones (1860 : 10) in their critique of 'The Foraminifera enumerated by Denys de Montfort' unfortunately shed little light on the problem . . .

'61. Vol. i, p. 330. 83^{e} genre. Reophax Scorpiurus. Soldani, Testaceogr. pl. 162, fig. K. This is a uniserial and, as it were, abortive variety of the arenaceous *Lituola nautiloidea*, and is of world-wide distribution in shelly deposits. Soldani's figure, true as to outline, fails to exhibit the sandy texture of the shell. De Montfort fancifully exaggerates the angularities of the segments of Soldani's drawing into doubly crossed chambers, "singulièrement quadrillées".

D'Orbigny refers the *Reophax* of De Montfort (under the terms "Réophage" and "Reophagus") to the Nodosariae in several of his notices of the synonyms of *Nodosaria*'.

From this historical résumé it is therefore not surprising that many discrete species, both fossil and Recent, have subsequently been referred to *Reophax scorpiurus* and that the true identity of the species is uncertain. Furthermore, the genus *Reophax* itself is in great need of revision. Recently, several authors, in particular Seiglie & Bermúdez (1971 : 221), have advocated that both *Reophax* and its type-species should be declared *nomina dubia*. However, in view of the fact that these names have been so much used in the literature, it is here proposed, in the interests of nomenclatorial stability, to redefine the genus on the basis of a neotype for *R. scorpiurus*.

(b) A neotype for *Reophax scorpiurus* de Montfort

According to de Montfort (1808 : 332) *R. scorpiurus* came from the Adriatic Sea, in sand. We have therefore examined a number of samples and faunal slides in the collections of the British Museum (Natural History) from beach sands of the Adriatic, for specimens of a *Reophax* which would best fit the figure of Soldani (1795 : pl. 162, fig. K) and the description of de Montfort. A neotype was finally chosen from a shallow water sample collected by H. Sidebottom off Corfu. Our thanks must go to Mr R. V. Melville, International Commission of Zoological Nomenclature, for his guidance in the choosing of this neotype, which is in keeping with Article 75 of the Code.

Reophax scorpiurus de Montfort
Figs 1–7, 12, 17

NEOTYPE. ZF 3985. From Corfu, S.E. Adriatic, shallow water. Heron-Allen & Earland 'Students' Collection', ex Sidebottom Collection. Figured by scanning electron microscopy in Figs 2, 5.

PARANEOTYPES. 12 specimens, three of which (ZF 3986–3988) are figured (Figs 1, 3, 4, 6, 7, 12, 17). From type-locality.

DESCRIPTION (NEOTYPE). Test free, uniserial; elongate and slender, slightly curved in lateral view, irregularly rounded in apertural view. Chambers four in number and rapidly increasing in size; overlap onto preceding chambers only slight. Early chambers more or less cylindrical, final one somewhat bulbous and ventricose, that is more rounded and wider on the inner side of the curvature of the test than on the outer side. Transverse sutures well defined, not oblique. The bulbous, ventricose ultimate chamber tapers gradually to its terminal and rounded aperture which is not produced. In course of ontogeny, position of aperture becomes more and more eccentric in respect to ventricose side of the chamber. Wall agglutinated, single-layered and imperforate, made up of relatively large angular quartz grains embedded in a clear, finely granular cement. Although the quartz grains surrounding the aperture are smaller than in the wall in general, the apertural rim remains rather coarsely textured.

DIMENSIONS (NEOTYPE). Length of test 700 μm. Chamber lengths from initial to ultimate: 100, 100, 150 and 350 μm; respective widths: 80, 120, 120 and 200 μm.

VARIATION (PARATYPES). Three of the 12 paraneotypes are illustrated by scanning electron microscopy in Figs 1, 3, 4, 6, 7, 12 and 17. The overall morphology is as described for the neotype, the tests closely resembling the scorpion's tail appearance of the specimen illustrated by Soldani (1795) and de Montfort (1808). Both 4 and 5-chambered forms occur, the lengths of the tests ranging between 550 and 1000 μm, about 700 to 800 μm being the average. In some paraneotypes the ventricose asymmetry of the final chamber is more distinct (e.g. Figs 3, 7) than in others.

REMARKS. The ventricose asymmetry seen in the final chamber and the absence of a produced aperture, as developed in *Hormosina*, are both important criteria in the generic definition of *Reophax*. These features are also well shown by the specimen from the Campos Shelf, Brazil, which although not as slender as the type-specimens, comes close to, and has been placed into *R. scorpiurus* (see Brönnimann, 1980, t-fig. 2, figs 1, 2). Many records of *R. scorpiurus,* however, are not conspecific with our type material. The specimen figured by Brady (1884, pl. 30, fig. 12) as *R. scorpiurus*, for instance, although possessing an asymmetric final chamber tapering to a terminal rounded aperture, has a much larger and more robust test with more voluminous chambers. It is described below as *Reophax bradyi* sp. nov. Also Loeblich & Tappan's (1964 : 216, fig. 128, 1) *R. scorpiurus* from the Gulf of Mexico is not conspecific with the neotype, and instead comes very close to *R. bradyi.* Cushman's (1920 : 6, pl. 1, fig. 7) specimen of *R. scorpiurus* from Albatross Stn. D2531 in the N. Atlantic, is probably a correct identification; he notes (p. 7) that the . . . 'early chambers (are) more or less indistinct, irregularly arcuate, later ones larger and more distinct, nearly in a straight line . . . .', but his later descriptions (1920, 1933 and 1940) include straight tests which belong to other hormosinid genera. It is beyond the scope of this paper to review critically all the very many references to *R. scorpiurus* in the literature. Most would, however, seem to be incorrect, based as they are on the wide concept of the species adopted by Brady (1884, pl. 30, figs 12–17) and subsequently by Cushman, and bear little relationship to the original description. Care must now be taken in assigning specimens to this taxon.

In view of the morphology shown by the neotype of *R. scorpiurus* and the foregoing discussion, the following emended diagnosis of *Reophax* is proposed.

(c) Emendation of the genus *Reophax* de Montfort

Family **HORMOSINIDAE** Haeckel, 1894

Genus ***REOPHAX*** de Montfort, 1808, emended Brönnimann & Whittaker, herein

1795 *Orthoceras* ? Bruguière; Soldani : 239
1808 *Reophax* de Montfort : 331
1826 *Nodosaria* Lamarck; d'Orbigny : 255
1858 *Proteonina* Williamson : 1
1860 *Lituola* Lamarck; Parker & Jones : 10
1874 *Silicina* Bornemann : 731
1887 *Reophaxopsis* De Folin : 127

The genera, *Ginesina* Bermúdez & Key, 1952 (type-species *G. delicatula*) and *Nodulina* Rhumbler, 1895 (type-species *Reophax dentaliniformis* Brady, 1881), synonymised with *Reophax* by Loeblich & Tappan (1964 : 216), are transferred to *Hormosina* (see below, p. 265).

EMENDED GENERIC DEFINITION. Test free, elongate, arcuate, consisting of a single series of chambers which normally increase in size during ontogeny and overlap to some degree onto the preceding chambers. Initial portion at least is incurved or early chamber arrangement suggests curvature. Adult chambers subglobular, cylindrical or pyriform, rounded or somewhat compressed in transverse section, asymmetric in side view, ventricose, heteropolar, devoid of internal structures, infolds of wall, and siphon. Wall agglutinated, single-layered, imperforate. Aperture terminal, subcircular, oval to elongate-oval.

TYPE-SPECIES. *Reophax scorpiurus* de Montfort. Recent. Adriatic Sea.

REMARKS. The test of the genus *Reophax*, as emended above, differs from that of *Hormosina* (Brady, 1879) in having an incurved early portion and ventricose asymmetry of the adult chambers as seen in lateral view. The type-species of *Hormosina*, *H. globulifera*, originally described by Brady from deep waters of the Atlantic and Pacific Oceans, is characterised by linearly arranged (occasionally irregularly disposed), globular, thin-walled, smooth-surfaced chambers (or rarely a single chamber) and a rounded terminal aperture produced on a distinct neck; the chambers, furthermore, are radially symmetrical. The generic differentiation between *Reophax* and *Hormosina* has in the past been unclear. It was dealt with by Brady (1884 : 325) when he wrote that . . . 'The genus *Hormosina* comprehends the moniliform section of the Trochammininae and occupies the same position in the group that *Reophax* takes amongst the rougher Lituolidae. Under ordinary circumstances, there is no difficulty in distinguishing the Hormosinae from their larger Lituoline isomorphs, by their thin walls and smooth, almost homogeneous tests, and amongst the smaller species by their regularity and symmetry of form'. Brady, however, still placed forms with radially symmetrical chambers in *Reophax* (a typical species being *R. dentaliniformis* Brady), whereas, work by one of us (Brönnimann, 1980) on Recent radially-symmetrical 'reophaxes' from the Campos Shelf of Brazil, has shown that Brady's criteria cannot be used in all cases to separate the two genera. Instead, the ventricose chamber asymmetry and initial curvature of the test, features highlighted in our emended generic diagnosis of *Reophax* (discussed further on p. 266, below), are much more reliable parameters. Wiesner (1931 : 89) arrived at similar conclusions to ourselves, but in spite of his observations, he still used the consistency of the wall as his main distinguishing feature.

As both *Ginesina* Bermúdez & Key (1952) and *Nodulina* Rhumbler (1895) have straight, linear tests and radially-symmetrical chambers, they are synonymized with *Hormosina,* instead of *Reophax* as was proposed by Loeblich & Tappan (1964 : 217).

Proteonina fusiformis Williamson, type-species of *Proteonina* (Williamson, 1858), from the Recent of Skye, was originally shown in side view (*op. cit.*, pl. 1, fig. 1) to possess an

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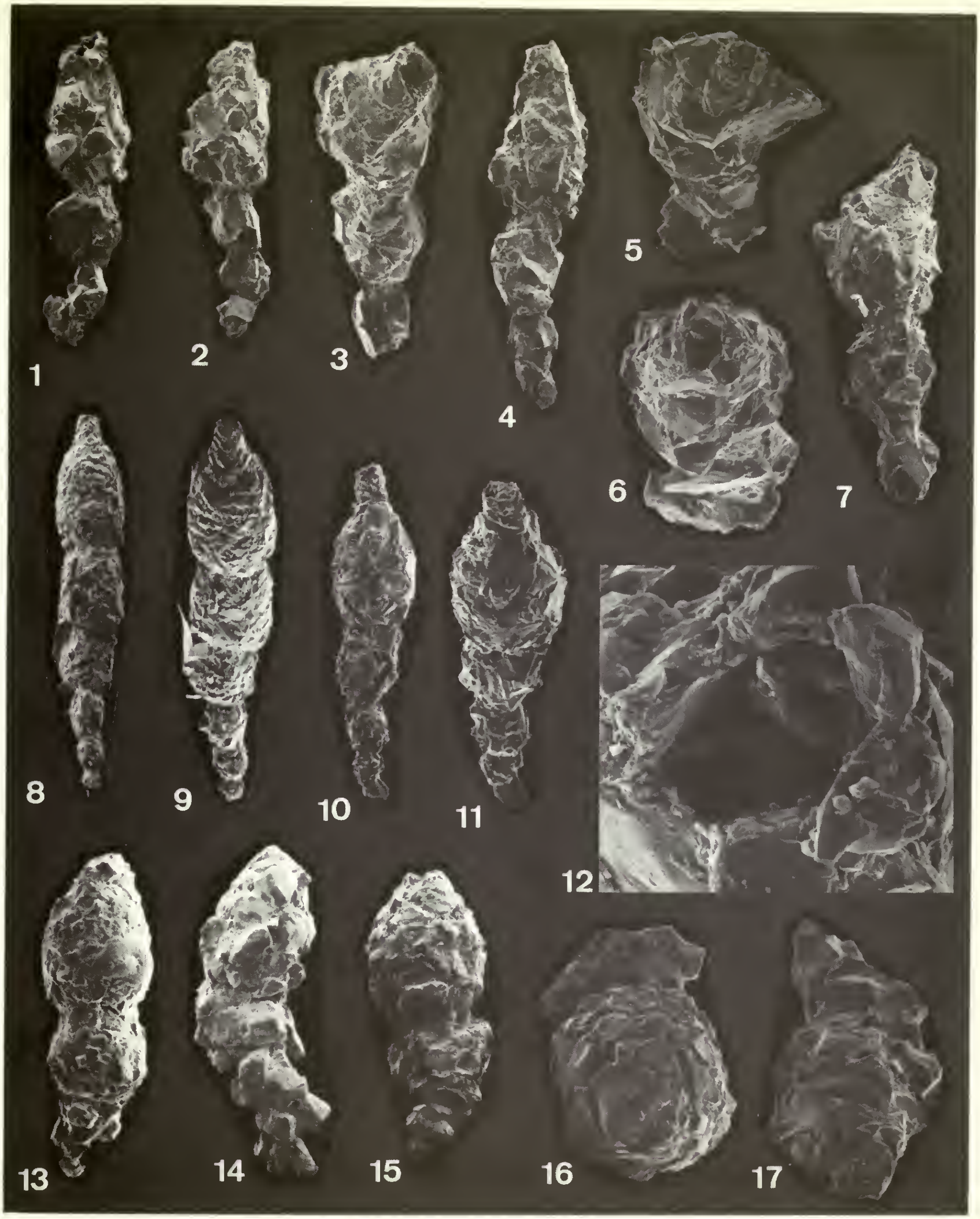
Figs 13–16 *Reophax bradyi* sp. nov. Fig. 13, Paratype (ZF 3993), side view. Fig. 14, Paratype (ZF 3994), side view. Figs 15, 16, Paratype (ZF 3995); side and oblique–apertural views. Fig. 13, from off Cronlin (?Crawlin) Island, Hebrides, N.W. Scotland, *Challenger* Collection. Figs 14–16, both from Heron-Allen & Earland Students' Collection, Mediterranean. Fig 13, 14, × 26; figs. 15, × 22; fig. 16, × 42.



Figs 1–7, 12, 17 *Reophax scorpiurus* de Montfort. Figs 2, 5, Neotype (ZF 3985); side and oblique-apertural views. Figs 1, 6, 12, Paraneotype (ZF 3986); side, oblique-apertural and detailed apertural views. Figs 3, 7, Paraneotype (ZF 3987); oblique-apertural and side views. Figs 4, 17, Paraneotype (ZF 3988); side and oblique-apertural views. All from Heron-Allen & Earland Students' Collection, Corfu, E. Mediterranean. Figs 1–4, 7, × 60; figs 5, 6, × 110; fig. 12, × 530; fig. 17, × 95.

Figs 8–11 *Hormosina dentaliniformis* (Brady). Figs 8, 9, Lectotype (ZF 3990); side and oblique-apertural views. (Specimen illustrated by Brady, 1884, pl. 30, fig. 21). Figs 10, 11, Paralectotype (ZF 3991); side and oblique-apertural views. Both from *Challenger* station 300, north of Juan Fernandez Island, E. Pacific. Fig. 8, × 25; fig. 9, × 30; fig. 10, × 42; fig. 11, × 54.

asymmetric ventricose ultimate chamber which gradually tapers to a rounded terminal aperture without a neck; the chamber is round in transverse section. There is some controversy as to whether this specimen is monothalamous or is subdivided. Williamson's figure does not appear to show sutures, but Loeblich & Tappan's (1955 : 7, pl. 1, figs 2, 3) lectotype, together with a specimen illustrated from Norway and referred by Höglund (1947, pl. 4, fig. 21) to this species, clearly do. After re-examining Williamson's material we have no hesitation in stating that *Proteonina* is a junior homonym of *Reophax*.

The genus *Sulcophax* Rhumbler (1931, *in* Wiesner) (type-species *S. claviformis*), from deepwater off Antarctica, is characterised by a linear test, heteropolar chambers and a sulcus-like depression across the terminal face in which an elongate apertural slit is situated. It is accepted as being distinct from *Reophax* by Loeblich & Tappan (1964 : 217, figs 128, 8a, b). Its chambers, although rounded in transverse section, are not radially symmetric, but through the development of a sulcus, dissymmetric. Hence, *Sulcophax*, though possessing a straight linear test, cannot be placed in *Hormosina* and is distinct.

Glaucoammina Seiglie & Bermúdez (1969), type-species *Reophax trilateralis* Cushman, from the Caribbean shelf seas, differs from *Reophax* in having a completely enrolled early stage. *Oblidolina* Brönnimann & Whittaker gen. nov., type-species *Reophax arcticus* Brady, from Arctic waters, lacks the incurved initial curvature of the test as seen in *Reophax* and is strongly laterally compressed (see p. 267, below).

Finally, there are certain Recent hormosinid species, previously referred to *Reophax*, such as *R. scotti* Chaster from shallow water off the coasts of the British Isles, which exhibit an ordered, tile-like arrangement of the quartz flakes making up the single-layered, imperforate wall (see Murray, 1971 : 17, pl. 1, figs 7, 8). The order in which the wall is constructed might be taxonomically significant at generic level, but at present there exists no comparative study of hormosinid wall textures which considers this potentially important criterion.

II. Some recent Hormosinid species in the collections of the British Museum (Natural History)

(a) On *Reophax bradyi* Brönnimann & Whittaker sp. nov.

Reophax bradyi sp. nov.

Figs 13–16

1884 *Reophax scorpiurus* de Montfort; Brady : 291 (*pars*), pl. 30, figs 12a, b, only. (*non* de Montfort, 1808).
1894 *Reophax scorpiurus* de Montfort; Goës : 24 (*pars*), pl. 6, figs 164–166 only.
1964 *Reophax scorpiurus* de Montfort; Loeblich & Tappan : 216, figs 128, 1.

DIAGNOSIS. A large, robust 4–6 chambered species of *Reophax* with inflated chambers throughout, Early portion of test curved, coarsely agglutinated, last two chambers straight, usually with finer agglutinant.

HOLOTYPE. ZF 3992. Off Cronlin (?Crawlin) Island, Hebrides, N.W. Scotland. *Challenger* Collection, ex Brit. Mus. (Nat. Hist.) slide no. ZF 2286. Specimen figured by Brady (1884, pl. 30, figs 12a, b), not re-illustrated in this paper.

DESCRIPTION (HOLOTYPE). Test uniserial, initially curved, later straight, composed of 6 chambers which increase rapidly in size, the last two chambers making up more than half of the test. Final chamber distinctly asymmetric in side view and ventricose (side which lies outside curvature of the test, almost straight, that on the inside, curved); early chambers more or less cylindrical. Sutures well defined, transverse, with little overlap of the chambers. Aperture terminal rounded and flush, rim made up of large angular quartz grains. Wall single layered and apparently imperforate, consisting of rather large angular quartz grains which are cemented by a very little light brownish organic material. Early chambers more coarsely agglutinated than final ones. Test overall yellow-brown in colour.

DIMENSIONS (HOLOTYPE). Maximum length of test 2100 μm; maximum length and width of final chamber 900 and 650 μm, respectively; maximum length of initial chamber 150 μm.

VARIATION (PARATYPES). A 5-chambered paratype (ZF 3993) from the type-locality is illustrated in Fig. 13. Its initial portion is only slightly curved but the final chamber shows the same ventricose aspect as the holotype. The initial portion is very coarsely agglutinated with angular quartz grains. The early portion is almost colourless, the later chambers are light yellowish. Its dimensions are: maximum length of test 1800 μm; maximum length and width of final chamber, respectively 900 and 600 μm. Two other paratypes, ZF 3994 and ZF 3995 are also figured. They are from Mediterranean waters (Siddall Collection) and have a similar morphology and dimensions to the Hebridean material.

REMARKS. The citations of Brady (1884), Goës (1894) and Loeblich & Tappan (1964) have probably been most widely used as a basis for *Reophax scorpiurus* in the literature. As none of them are conspecific with the neotype of de Montfort's species as described above, a new species is proposed to clarify the situation. Other specimens in the *Challenger* Collection referred by Brady to *R. scorpiurus* (e.g. Brady, 1884, pl. 30, figs 13–17), by their overall morphology and agglutination of the wall, belong neither to *R. scorpiurus* s.s. nor to *R. bradyi* and need further study beyond the scope of this paper.

(b) On *Hormosina dentaliniformis* (Brady)

Brady (1881 : 49) described this species as . . . 'a small, delicate variety of *R. scorpiurus*, but more slender and regular in contour . . .', but he did not illustrate it. In the Challenger Report (1884 : 293)he refers to it as a '*Dentalina*-like modification of *Reophax scorpiurus*', adding that . . . 'its home is on the deep sea-bottoms, and out of twenty-one stations at which its presence has been noted, only four have a depth of less than 1000 fathoms, whilst seven are above 2000, and two above 3000 fathoms'. He illustrates two specimens without defining a holotype. In this paper the opportunity is taken to choose a lectotype, and to re-describe and illustrate the species.

Family **HORMOSINIDAE** Haeckel, 1894

Genus ***HORMOSINA*** Brady, 1879

TYPE-SPECIES: *Hormosina globulifera* Brady, 1879. Recent. Atlantic and Pacific Oceans.

Hormosina dentaliniformis (Brady)

Figs 8–11

1881 *Reophax dentaliniformis* Brady : 49.
1884 *Reophax dentaliniformis* Brady; Brady : 293, pl. 30, figs 21, 22.

LECTOTYPE. ZF 3990. From *Challenger* station 300, north of Juan Fernandez Island, E. Pacific, depth 1,375 fathoms (2,515 m), ex Brit. Mus. (Nat. Hist.) slide no. ZF 2265. Figured by scanning electron microscopy in Figs 8, 9; originally illustrated by Brady, 1884, pl. 30, fig. 21.

DESCRIPTION (LECTOTYPE). Test long, slender and tapering, consisting of 6 pear-shaped or cylindrical chambers arranged more-or-less in a straight line and rapidly increasing in size, separated by rather indistinct transverse sutures. In side view, chambers are radially symmetrical, heteropolar and have little overlap onto the preceding ones, ultimate chamber tapering gradually into a distinct neck which is produced and has a rounded terminal aperture; in transverse section, chambers rounded. Agglutinant consists of large angular and rounded grains of quartz, with black, yellow and brown mineral grains; cement white.

DIMENSIONS (LECTOTYPE). Length of test 2050 μm. Chamber length, from initial to ultimate, 150, 200, 250, 300, 450 and 700 μm; respective widths, 110, 150, 220, 350, 350 and 400 μm. Length of apertural neck 150 μm, outside diameter of aperture 120 μm.

VARIATION (PARALECTOTYPES). The figured paralectotype (ZF 3991), one of a group of 24 specimens from slide ZF 2265, N of Juan Fernandez, is 1060 μm long. Lengths of individual chambers from initial to ultimate, are 50, 100, 170, 230 and 510 μm. The maximum diameter of the final chamber is about 290 μm and that of the rounded aperture, including the thick wall, is 70 μm. The length of the tubular apertural neck is 140 μm. The specimen is very similar in morphology to the lectotype, but has five chambers and is much smaller. The remainder of the paralectotypes vary in length between 700 and over 2000 μm and the number of chambers varies from two to six. Other specimens in the Museum collections from *Challenger* dredgings both in the Atlantic and Pacific, show very little morphological variation.

REMARKS. The rectilinear test, radial symmetry of the chambers and produced apertural neck clearly place this species in *Hormosina*, rather than in *Reophax* as redefined above. The new genus *Nodulina*, proposed for this species by Rhumbler (1895), is unnecessary.

(c) ***Oblidolina*** **Brönnimann & Whittaker gen. nov.**

Family **HORMOSINIDAE** Haeckel, 1894
Genus ***OBLIDOLINA*** gen. nov.

GENERIC DEFINITION. Test free; viewed laterally, elongate, tapering, consisting of a single series of chambers arranged in a straight line and which normally increase in size as added and overlap to some degree on the preceding ones; viewed aperturally, elongate-ovate in shape. Postembryonic chambers strongly compressed in edge view; radially asymmetric, heteropolar, devoid of inner structures, infolds of the wall, and siphon. Wall agglutinated, single layered, imperforate. Aperture terminal, oval to lozenge-shaped in outline, may be slightly produced.

NAME. *Oblido*, latin, to squeeze together. It refers to the highly compressed nature of the test.

TYPE-SPECIES. *Reophax arcticus* Brady, 1881. Arctic Sea.

REMARKS. The agglutinated wall of the genera *Reophax*, *Hormosina* and *Oblidolina* is single layered and imperforate. The chemical composition of the organic substance in which the agglutinant is incorporated and the degree of order in which it is arranged, are not considered in this purely morphological classification. Once the taxonomic significance of these criteria is better understood it may be possible to introduce a more refined system than that proposed here. Because the constitution of the wall is more or less the same throughout the Hormosinidae, the three genera reviewed in this paper are differentiated by gross morphological features as follows.

The primary feature of taxonomic importance is the radial symmetry or asymmetry of the adult chambers in respect to the axis of growth. Radial or monaxial heteropolar symmetry in the sense of Hyman (1940 : 19), here applied to chamber organization, occurs in *Hormosina*. Asymmetry or bi-radial symmetry or dissymmetry in the sense of Hyman (1940 : 19, 20) are seen in *Reophax*, *Sulcophax* and in *Oblidolina*, where the longitudinal axes of the adult chambers are heteropolar.

The second ranking element is the lateral compression of the postembryonic chambers. It is present throughout the test of *Oblidolina*, and normally absent in *Reophax*, but occasionally the ultimate chamber may show slight lateral compression. This lateral compression does not occur in *Hormosina*, although Höglund (1947 : 92) mentioned that *Reophax nanus* Rhumbler, which we would refer to *Hormosina*, may show a slight compression. Haynes (1973 : 22) also described specimens of *H. nana* (as *Reophax arctica* Brady) from Cardigan Bay, Wales, as 'slightly compressed'.

The initial curvature of the test is the third classificatory feature in order of importance. The initial portion of *Reophax* is always incurved to some degree. *Hormosina* and *Oblidolina* are represented by straight or almost straight tests, devoid of any initial curvature.

Normally, the generic determination of a given species does not pose any problems. However, if one of the three critical features listed above is not well developed, or ambiguously developed—such as the ventricose asymmetry of the adult chamber(s) in certain species of *Reophax*, or where a slight compression of a chamber may occur in a few species of *Hormosina*—then problems might arise concerning the generic assignment of the species. If whole populations are considered such problems do not occur.

The apertural features, in particular the form of the opening, whether it is produced or not, or contained in a sulcus or not, as well as details of the chamber form (but *not* concerned with symmetry or asymmetry), and the number of chambers, etc., enter only in the diagnosis of the species.

(d) On *Oblidolina arctica* (Brady)

Apart from *Hormosina nana* (Rhumbler), *Oblidolina arctica* (Brady) is probably the most frequently recorded hormosinid species from Arctic waters. It was first described by Brady (1881*a* : 405, pl. 21, figs 2a, b) under the name of *Reophax arctica*, as . . . 'Test elongate, tapering, often more or less irregular, compressed, only slightly constricted at the septal lines. Segments numerous; septation indistinct; aperture simple; wall arenaceous, very thin. Length 0·3 millim.'. The material came from the Austro-Hungarian North Polar Expedition, where it was said (*op. cit.* : 405) to be . . . 'an exceedingly minute and obscure species, which may be regarded as a sandy isomorph of *Lingulina*. With the exception of a single specimen from Station 504, and one which had been previously recorded, without a specific name, from Capt. Markham's soundings, all the specimens are from Station 503, so that the distribution appears confined to the Novaya Zemlya Sea'.

Oblidolina arctica (Brady)
Figs 18–32

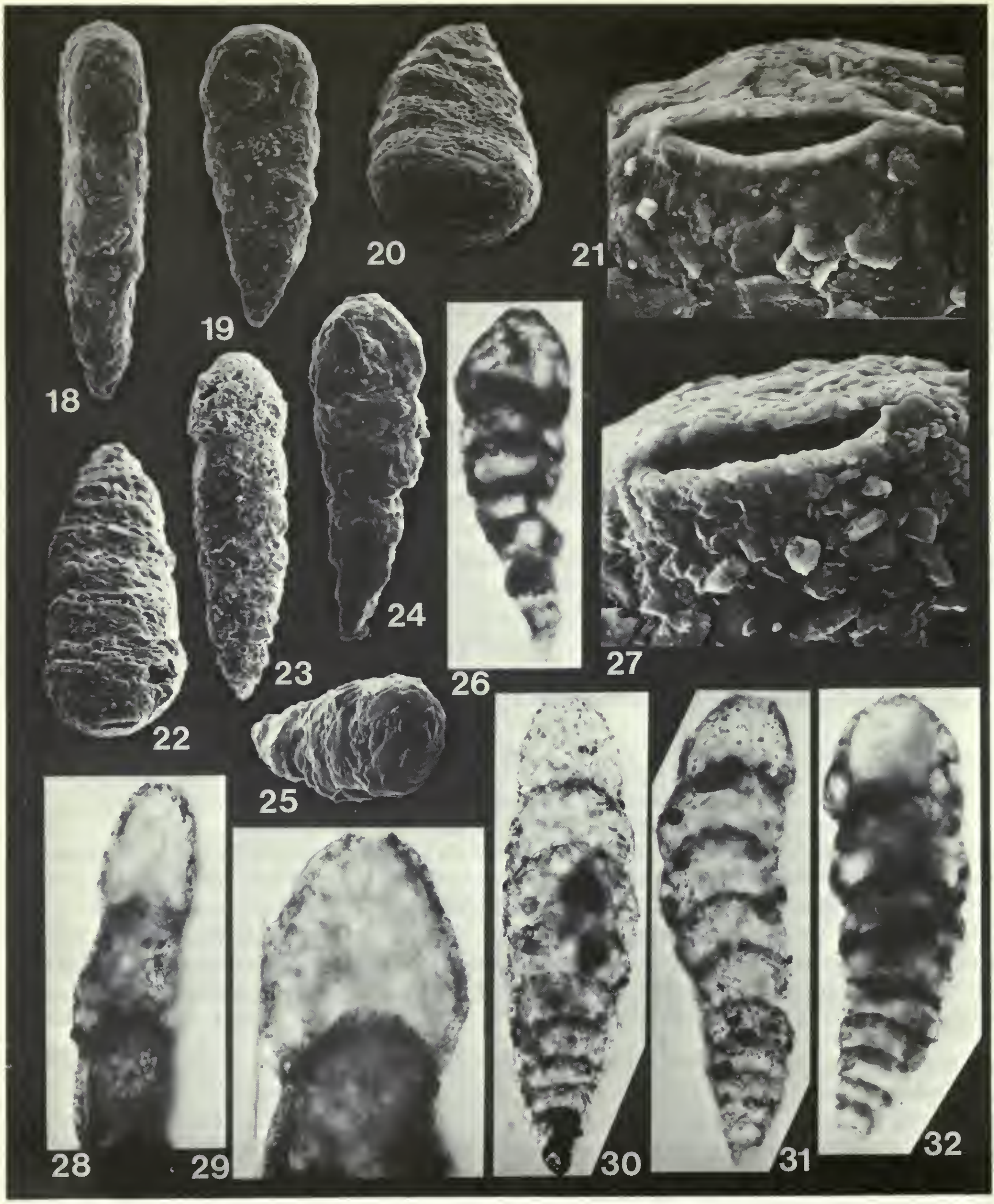
1881*a* *Reophax arctica* Brady : 405, pl. 21, figs 2a, b. (English version).
1882 *Reophax arctica* Brady; Brady : 11, pl. 2. figs 2a, b. (German translation).
?1929 *Bigenerina delicatula* Cushman & Kellett : 3 (*pars*), pl. 1, figs 5a, b only.
?1952 *Reophax arctica* Brady; Parker : 395, pl. 1, figs 6, 7.
non 1957 *Reophax arctica* Brady; Boltovskoy : 18, pl. 3, figs 1–4.
non 1973 *Reophax arctica* Brady; Haynes : 22, pl. 3, figs 8–12; pl. 6 figs 4, 5, 7.
1978 *Reophax arctica* Brady; Schafer & Cole : 29, pl. 2, fig. 5.

LECTOTYPE. ZF 3996. From Austro-Hungarian North Polar Expedition station 503, off Novaya Zemlya, Arctic Ocean, lat. 76°25′N, long. 62°43′E, depth 70 fathoms (130 m), ex. Brit. Mus. Nat. Hist. slide no. 1955.101.714–715. Figured by scanning electron microscopy in Figs 18–21.

DESCRIPTION (LECTOTYPE). Test wedge-shaped in side and edge view, made up of a tapering linear series of 9 chambers of which the final three make up about half the test; in apertural view, elongate-ovate with rounded peripheries. Proloculus subglobular; remaining chambers distinctly compressed, dissymmetric or bilaterally symmetric, heteropolar, not radially symmetric (excepting possibly the proloculus), and at least the adult chambers wider than high. Transverse sutures straight, indistinct in the early portion of the test, but well defined later on. Overlap of chambers very small. Aperture, a lozenge- or diamond-shaped elongate slit produced only slightly. Agglutinated wall rather smooth, single-layered and imperforate. Agglutinant a fine-grained groundmass in which larger quartz grains and flakes are incorporated; there is very little organic cement. Colour or test, brownish-grey.

DIMENSIONS (LECTOTYPE). Length of test 300 μm. Length, width and thickness of final chamber, respectively 80, 100 and 70 μm. Diameter of proloculus 20 μm. Respective length and width of aperture, 40 and 7 μm.

VARIATION. The paralectotype (ZF 3998) shown in Figs 24, 25, also comes from the Brit. Mus. Nat. Hist. slide no. 1955.101.714–715, from the type-locality. It is 260 μm in length.



Figs 18–32 *Oblidolina arctica* (Brady). Figs 18–21, Lectotype (ZF 3996); edge, side, oblique-apertural and detailed apertural views. Figs 22, 23, 27–29, ZF 3997; oblique-apertural, side and detailed apertural views; edge and side views of final chambers in immersion oil. Figs 24, 25, Paralectotype (ZF 3998); side and oblique-apertural views. Figs 26, 30–32, side views of four topotypes in immersion oil. Figs 18–21, 24, 25, both from Austro-Hungarian North Polar Expedition, station 503, Novaya Zemlya (U.S.S.R.), Arctic Ocean. Figs 22, 23, 27–29, from the Restigouche River, New Brunswick, E. Canada, material donated by Dr C. T. Schafer. Figs 26, 30–32, all from Austro-Hungarian North Polar Expedition, station 503, Naturhistorisches Museum, Vienna, slide no. 1978/1953. Fig. 18, × 185; fig. 19, × 150; fig. 20, × 210; fig. 21, × 925; fig. 22, × 220; fig. 23, × 160; figs 24, 25, × 190; fig. 26, × 360; fig. 27, × 1450; fig. 28, × 250; figs 29, 31, × 340; fig. 30, × 370; fig, 32, × 400.

In the Naturhistorisches Museum, Vienna, there exists a further slide prepared by Brady, with 12 additional paralectotypes from Austro-Hungarian North Polar Expedition station 503. As photography or preparation of this material was not allowed, Dr F Rögl kindly provided the authors with ten topotypic specimens picked out of the original sample (Naturhistorisches Museum, Vienna, slide no. 1978/1953). All these topotypes are compressed, but the degree of compression is variable. Irregularities of growth are expressed either by a slight curvature of the test or by sudden changes in the size and shape of a chamber, or both. Five of the topotypes were placed in a clearing medium and four of them photographed in transmitted light are illustrated in Figs 26, 30–32. They show that the ultimate chamber is invariably wider than it is high and its periphery, as seen in edge and apertural views, is rounded. The proloculus is subglobular with a very thin wall less than 1 μm thick, of clear brownish appearance, almost devoid of agglutinant. In lateral view, the position of the aperture, slightly produced and on average about 20 μm in length, is suggested by a flattening of the terminal portion of the final chamber. The walls of the test are thin, not more than 5 μm thick in the final chamber and agglutinated by rather large quartz flakes and dark mineral grains; there is only very little organic cement. The agglutinant, though consisting of relatively large components, appears to be distributed in such a way that it produces a rather smooth surface which is light grey in colour. The dimensions of the five topotypes, measured in oil, are given below, together with those of the lectotype for comparison.

Specimen	Length of test	Diameter of proloculus including the wall	Final chamber Width	Final chamber Length	No. of chambers
Topotype 1	200 μm	30 μm	80 μm	40 μm	7
Topotype 2	270	20	65	50	9
Topotype 3	230	?	70	55	?11
Topotype 4	180	20	80	40	8
Topotype 5	250	10	80	50	11
Lectotype	300	20	100	80	9

Dr C. T. Schafer, Bedford Institute of Oceanography, Dartmouth, Canada, has sent us a number of specimens determined by him as *Reophax arcticus* Brady from the Restigouche River, New Brunswick, Canada. They are very similar in overall morphology to the lectotype, paralectotypes and topotypes from station 503, Novaya Zemlya, in that they are distinctly compressed and exhibit a somewhat serrated outline in side view; the tests are also occasionally, tortuous or slightly curved and show the growth irregularities first mentioned by Brady (1881*a*). Their colour is grey brown and the agglutinant contains numerous dark mineral grains. One of the specimens has been illustrated by scanning electron microscopy in Figs 22, 23, 27, whilst another was photographed in clearing oil and is shown in Figs 28, 29. The dimensions of seven specimens from the Restigouche River, measured in oil, are given below. An asterisk denotes the proloculus is missing.

Specimen	Length of test	Diameter of proloculus including the wall	Final chamber Width	Final chamber Length	No. of chambers
1	400 μm	20 μm	80 μm	50 μm	12
2	675	25	100	110	15
3	325	20	70	60	10
4	220	—	90	50	9*
5	300	—	80	65	9*
6	265	15	95	50	10
7	295	15	75	60	11

The individual listed as specimen no. 2 refers to a very long, tortuous test with a final growth stage of 3 chambers which are smaller than the preceding ones and almost equidimensional when seen in lateral view. Measured edgeways it has a maximum thickness of 70 μm against a lateral width of 100 μm. The elongate aperture is 25 μm long and about 15 μm wide. In specimen no. 3 the widest chamber is not the final one but the 9th chamber with a width of 90 μm. This tendency in larger individuals to produce smaller final chambers has not been observed in the type-material.

REMARKS. Because the highly compressed, almost straight test, with radially asymmetric chambers, does not correspond to *Reophax s.s.*, as redefined, nor readily to any other hormosinid genus, our new genus *Oblidolina* is justified.

Although commonly recorded from Arctic and both North and South Atlantic waters (see Haynes, 1973), many records are in error and now need careful comparison with the lectotype. For this reason our synonymy is restricted to selected references which are discussed herein.

Possibly the specimen described and illustrated by Cushman & Kellett (1929 : 3, pl. 1, figs 5a, b) from the west coast of South America, as the 'Adult. Uniserial stage' of *Bigenerina delicatula* Cushman & Kellett, may be *Oblidolina arctica.* It shows the same compressed uniserial test and lozenge-shaped aperture and is quite clearly different from the biserial test of *B. delicatula.* The specimens determined by Parker (1952 : 395, pl. 1, figs 6, 7) as *Reophax arctica* may be conspecific. However, nothing is said in her description about the compression of the test nor is the edge view illustrated, and without seeing her original material it is impossible to be certain. One of us (P. B.) has examined the specimens from the mouth of the Río de la Plata, Argentina, determined by Boltovskoy (1957 : 18, pl. 3, figs 1–4) as *R. arctica.* In transverse section the chambers are usually rounded, however, although the adult chambers may sometimes show a slight lateral compression. The aperture is rounded to oval in shape and only slightly produced and is quite unlike that of *Oblidolina arctica.* We are of the opinion that they probably belong to *Hormosina nana* (Rhumbler). They are illustrated by scanning electron microscopy with further comments in Brönnimann (1980, t-fig. 6, figs 3–5, 11, 13–15, 17, 18).

Material

The material illustrated in this paper, with the exception of the specimens (1978/1953) returned to the Naturhistorisches Museum, Vienna, are housed in the collections of the Protozoa Section, Department of Palaeontology, British Museum (Natural History), registered numbers ZF 3985–ZF 3998 inclusive.

Acknowledgements

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The coelenterate taxa of Joshua Alder

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Introduction

Joshua Alder (1792–1867) is undoubtedly remembered more for his contributions to mollusc and tunicate biology, published with Albany Hancock, than for his work on hydroids. This is made clear in the bibliographic accounts of Alder by Embleton (1867) and Goddard (1929). Alder's important contributions to hydroid systematics, which appeared during the years 1856 to 1867, were soon overshadowed by the exhaustive monograph of the group by Hincks (1868). But during those twelve years, from the age of sixty-four onwards, Alder proposed one genus and twenty-seven species of hydroids and two species of anthozoans. Most were based on material he had collected from the shores and coastal waters of Northumberland. Twelve of the hydroid species are still regarded valid. Three others are problematical, and the rest are today thought invalid.

Hincks (1868) stated that Alder was 'foremost amongst those to whom' he had 'been indebted for help' in the preparation of his own monograph, and that he had profited from having seen Alder's collections. Several of the species described by Alder and still regarded valid are distributed widely in the Atlantic and other oceans and Alder's descriptions, being the earliest, are important.

A fair criticism of much systematic hydroid literature of the past hundred years is that scant attention has been paid to type material. Except for a few specimens the types in the Alder collections have been overlooked. Thus it is important to note that type specimens of most of the hydrozoan and anthozoan species proposed are still preserved. They are distributed about equally between the British Museum (Natural History) [BMNH] in London and the Hancock Museum, University of Newcastle upon Tyne [HM].

The Alder collection in the Hancock Museum is remarkable not only for its types, but for the range of species represented by non-type material. There is probably no older collection of British hydroids including such a wide range of species. It is probably also the oldest spirit-preserved hydroid collection of its size in Britain. Alder's extensive collection of 'Bryozoa' is preserved alongside but like the hydroid collection has been ignored by most taxonomists.

The hydroid material is preserved in a variety of ways. In each of the two museums there are both herbarium specimens and others in spirit, while in the BMNH alone there are a few dry specimens in boxes. Strangely, the only microslide preparations are those made during the present study (see under *Laomedea neglecta*).

Material of species represented in the HM collections but not first described by Alder is not mentioned unless it is type or potentially so (p. 287). In addition the species *Gonothyraea loveni* (Allman, 1859*a*) is mentioned since Alder was among the first to consider it distinct (p. 285).

The nominal taxa discussed are listed under their original names, but in their current systematic order. Neotype material is designated of *Laomedea neglecta* (p. 284). The reference list includes all publications by Alder concerning coelenterates and we have determined their correct dates of publication. The scientific names of British algae and non-coelenterate animals follow Parke & Dixon (1968) and Marine Biological Association (1957).

The word Northumberland is used in the old sense. It thus takes in the region around Cullercoats, where Alder collected many of the specimens discussed below. Cullercoats is

Bull. Br. Mus. nat. Hist. (Zool.) **39** (5) : 273–291

Issued 18 December 1980

today more correctly included in the new County of Tyne and Wear; but in the present context that is confusing.

Annotated catalogue of type material

Class ANTHOZOA

Order ACTINIARIA

Family METRIDIDAE

'Actinia pellucida' Alder, 1857*a*

Actinia senilis: Linnaeus, 1767 : 1088.
Actinia pellucida Alder, 1857*a* : 133–134.
Metridium senile: Stephenson, 1935 : 214–232, 392 (syn. *Actinia pellucida* Alder).

TYPE LOCALITY. Cullercoats, Northumberland; on shells of *Neptunea antiqua* (Gastropoda); coll. J. Alder.

TYPE MATERIAL. Not found.

STATUS. Junior synonym of *Metridium senile* (Linnaeus, 1767) (see Stephenson, 1935).

REMARKS. Alder based the description of this species on small specimens of the plumose anemone, *Metridium senile*. The combination *Actinia pellucida* had been used by authors earlier than Alder, and so is not available; but there is no current reason to propose an alternative name since the species is invalid. Details of the primary homonymy are given by Williams (in prep.).

Order PENNATULACEA

Family PENNATULIDAE

'Pennatula mollis' Alder, 1867

Pennatula phosphorea Linnaeus, 1758 : 818; Pax, 1934 : 287–316, figs 197–199, 202–203, 209–211.
Pennatula mollis Alder, in Norman, 1867 : 196, 206 (nom. nud.); Alder, 1867 : 207.

TYPE LOCALITY. Hebrides (Alder, 1867). Norman (1867) implied that the type material came from near the Isle of Skye, but his wording was ambiguous and a wider interpretation, 'Hebrides', can equally be inferred.

SYNTYPES. **BMNH** Two well preserved specimens in spirit, coll. J. G. Jeffreys, Hebrides, 1866; formerly in A. M. Norman collection; 1898.5.5.31–32.

OTHER MATERIAL. **HM** Four *Pennatula phosphorea* colonies in one jar, labelled '*Pennatula*, Hebrides'. A second label was faded and illegible. Although these four colonies are possibly part of the type series of *P. mollis* there is no proof. Also in the HM are four non-type colonies labelled '*Pennatula phosphorea* Linn., Cullercoats, Alder coll.'.

STATUS. Junior synonym of *Pennatula phosphorea* Linnaeus, 1758.

REMARKS. Despite the many revisions of the genus *Pennatula* appearing over the past 100 years *P. mollis* Alder has escaped attention. But the type material is identical with *P. phosphorea*, and *P. mollis* can be referred to it.

Class HYDROZOA

Order HYDROIDA

Family CORYMORPHIDAE

Corymorpha nana Alder, 1857*a*

Hydractinia sp. Johnston, 1847 : 463, fig. 79a.
?Euphysa aurata Forbes, 1848 : 71–72, pl. 13, fig. 3a-e.
Corymorpha nana Alder, 1857*a* : 108–109, pl. 9, figs 7–8.
?Corymorpha aurata: Naumov, 1960 : 210–211, figs 95–96 (syn. *C. nana* Alder); Naumov, 1969 : 210, figs 95–96 (syn. *C. nana* Alder).

TYPE LOCALITY. Newbiggin, Northumberland 'among sea-refuse brought in by the fishing boats'; June 1843; 'two specimens'.

MATERIAL. **HM** *Spirit* Two specimens, one (syntype) dried up, labelled '*Corymorpha nana* Alder, Newbiggin'; the second (non-type) well preserved, labelled '*Corymorpha nana* Alder, Cullercoats'.

STATUS. Problematical. Hartlaub (1907 : 81) tentatively linked *Corymorpha nana* hydroid with the medusa *Euphysa aurata* Forbes, 1848. But Rees (1938 : 25) and Russell (1953 : 84) doubted the two were conspecific. Meanwhile Vervoort (1946 : 114) and Naumov (1960 : 210–211; 1969 : 228) accepted the synonymy. Werner (1959 : 35) reared young polyps from *E. aurata* medusae but did not describe the polyps in detail, and the relation to *C. nana* was still in doubt. Although the two might well prove the same there is no published proof. But C. Edwards (pers. comm.) has new evidence that *aurata* and *nana* are conspecific.

Calder (1975 : 292) has suggested that *Dahlgrenella farcta* Miles, 1937, is also conspecific.

REMARKS. Alder sent one of the two specimens collected from Newbiggin, Northumberland, in June 1843, to George Johnston, together with a brief description and sketch. Alder (1857*a*) records that the specimen did not reach Johnston in a fit state for examination, but Alder's description and sketch were still mentioned by Johnston (1847) in his account of the species. Although provisionally referring it to the genus *Hydractinia*, Johnston did not provide a specific name.

The HM specimen from Newbiggin is probably the second of the two mentioned in the original description. Although dried, it still resembles the original illustrations and can be considered one of the two type specimens. We have not found the other.

Family **TUBULARIIDAE**

Tubularia simplex Alder, 1862*c*

Tubularia simplex Alder, 1862*c* : 232–233, pl. 8, figs 3–4; Hincks, 1868 : 121, pl. 22, figs 1, 1a; Naumov, 1960 : 218–219, fig. 107; Naumov, 1969 : 237, fig. 107.

TYPE LOCALITY. Cullercoats, Northumberland; 'on old shells and other marine bodies from deep water'.

SYNTYPES. **HM** *Spirit* Three unbranched stems, one with a well preserved hydranth; labelled '*Tubularia simplex* Alder' and '*Tubularia simplex* Cullercoats, figured'. *Herbarium* Five unbranched stems on one sheet, labelled '*Tubularia simplex*, Cullercoats'.

STATUS. Problematical. Although *T. simplex* might prove valid (e.g. Hincks, 1868; Naumov, 1960, 1969) Vervoort (1946) referred the species to *T. larynx* Ellis & Solander, 1786.

REMARKS. The HM material is the syntype series. The spirit preserved specimens probably formed the basis of the original illustration since the well preserved hydranth closely resembles the published drawing.

The status of *T. simplex* is unclear, although the distinction from *T. larynx* may well be as described by Naumov (1960, 1969). The descriptions of Alder and Naumov, and the few non-type BMNH specimens identified as *T. simplex*, suggest that there are two species. *T. simplex* is reportedly smaller in all proportions, has fewer tentacles in the oral circlet and (Naumov) is said to have medusoid gonophores. But it may yet prove to have been based on small *T. larynx* material, as implied by Vervoort (1946). *T. simplex* has been recorded only a few times from British waters.

Genus *'VORTICLAVA'* Alder, 1856*a*

Tubularia Linnaeus, 1758 : 803; Brink, 1925 : 199 (syn. *Vorticlava* Alder, 1856*a*).
Vorticlava Alder, 1856*a* : 353; Alder, 1857*a* : 100; Alder, 1857*b* : 245.

TYPE SPECIES. *Vorticlava humilis* Alder, 1856*a*, by monotypy.

STATUS AND REMARKS. The type species of *Vorticlava* has been referred to *Tubularia* Linnaeus, 1758, by recent authors (see notes under *V. humilis*) and *Vorticlava* need not be recognized.

'Vorticlava humilis' Alder, 1856*a*

Tubularia larynx Ellis & Solander, 1786 : 31–32; Vervoort, 1946 : 103 (syn. *V. humilis* Alder).
Vorticlava humilis Alder, 1856*a* : 353–354, pl. 12, figs 1–4; Alder, 1857*a* : 100–101, pl. 3, figs 1–4; Alder, 1857*b* : 245; Alder, 1857*c* : 90.

TYPE LOCALITY. Cullercoats, Northumberland; 'on a branch of *Corallina officinalis*'; intertidal.

TYPE MATERIAL. Not found.

STATUS. The material described by Alder as *V. humilis* was immature, and Hincks (1868) thought that if the adult were found it would prove to be a species which was already known. Brink (1925) thought it might be *Tubularia larynx* Ellis & Solander, 1786, and the two were treated as conspecific by Vervoort (1946).

REMARKS. *Vorticlava humilis* Alder, 1856*a*, should not be confused with *Tubularia humilis* Allman, 1864*b*, which it happens has also been referred to *T. larynx* (e.g. Vervoort, 1946).

Family **ZANCLEIDAE**

Tubularia implexa Alder, 1856*b*, and ***'Coryne pelagica'*** Alder, 1857*a*

Zanclea costata Gegenbaur, 1856 : 229–230, pl. 8, fig. 4; Russell, 1953 : 99–105, pl. 4, figs 1–3, text-figs 43–48; Rees & Roa, 1966 : 40; Russell, 1970 : 234.
?*Tubularia implexa* Alder, 1856*b* : 439–440; Alder, 1857*a* : 108, pl. 9, figs 3–6; Alder, 1857*b* : 245.
Coryne pelagica Alder, 1857*a* : 103, pl. 9, figs 1–2.
Coryne implexa: Alder, 1862*b* : 312 (syn. *C. pelagica*); Alder, 1862*c* : 227–228, pl. 10, fig. 4 (syn. *C. pelagica*).
Zanclea implexa: Allman, 1864*a* : 357; Rees & Roa, 1966 : 39–41.

TYPE LOCALITIES. (i) *Tubularia implexa* 'Thirty miles off Holy Island', Northumberland, 'on an old anchor brought in by fisherman from forty fathoms water'; coll. R. Howse. (ii) *Coryne pelagica* Cullercoats, Northumberland, 'deep water', on shells of the gastropod, *Neptunea antiqua*.

MATERIAL. **HM** *Spirit* Formerly preserved in four tubes. The first contained a tangled mass of hydroid material (syntypes of *T. implexa*) labelled '*Zanclea implexa* Alder' and '*Coryne implexa* Mr Howse'. The second tube was totally dry and contained only a piece of wood; labelled '*Zanclea implexa* Alder' and '*Coryne implexa*, Seaham, 25–30 fathoms, Mr Hodge'. The third contained only a small piece of rock and was labelled '*Zanclea implexa* Alder' and '*Coryne pelagica implexa*, Cullercoats'. The fourth tube was empty, but was labelled '*Zanclea implexa* Alder' and '*Coryne implexa (pelagica)*, Seaham harbour'. *Herbarium* Many hydrocauli (syntypes of *T. implexa*), labelled '*Coryne implexa*, deep water, Northumberland, R. Howse'.

BMNH *Spirit* Several hydrocauli labelled '*Zanclea implexa* Alder, Northumberland, Mr Alder', received as part of the A. M. Norman collection, 1912.12.21.412. *Dry, in box* Many hydrocauli, labelled '*Tubularia implexa* Alder, Northumberland', J. Alder collection, 1857.8.3.53.

STATUS. Russell (1953) referred both *T. implexa* Alder, 1856*b*, and *C. pelagica* Alder, 1857*a*, to *Zanclea costata* Gegenbaur, 1856; but Rees & Roa (1966) maintained that the species were distinct. Later Russell (1970) refrained from comment and at present it is not clear whether *implexa* and *costata* are two species or one. If they prove conspecific the senior name would be *costata* since Gegenbaur's paper was issued on 12 July 1856, while Alder's (1856*b*) did not appear until December of that year.

REMARKS. The HM herbarium specimen and the first tube of spirit material are almost certainly part of the syntype series of *Tubularia implexa* Alder. The BMNH specimens might also be type. The third and fourth HM tubes might have contained type material of *C. pelagica*, but this was not certain.

Family **HYDRACTINIIDAE**

Hydractinia areolata Alder, 1862*a*

Hydractinia areolata Alder, 1862*a* : 144; Alder, 1862*b* : 311–312, pl. 13, figs 1–4; Alder, 1862*c* : 225–226, pl. 9, figs 1–4; Alder, 1863*a* : 314–315, pl. 14, figs 1–4; Alder, 1864 : 192.
Podocoryne areolata: Hincks, 1868 : 32–34, pl. 6, figs 1, 1a; Edwards, 1972 : 97–135, figs 1–3.

TYPE LOCALITY. Cullercoats, Northumberland, 'deep water'; on a small specimen of the bivalve, *Natica alderi*.

TYPES. **HM** *Spirit* Two colonies (holotype and ?paratype) on two empty shells of *Natica alderi*, labelled '*Podocoryne areolata* Alder' and '*Hydractinia areolata*, Cullercoats'.

STATUS. Widely regarded as valid. The species was referred to the genus *Podocoryne* Sars, 1846, by Hincks (1868). Edwards (1972) provided a detailed synonymy.

REMARKS. Edwards (1972) thought one of the HM colonies to be that originally figured and identified it as holotype. The status of the second colony was uncertain.

Family **BOUGAINVILLIIDAE**

Atractylis arenosa Alder, 1862*a*

Atractylis arenosa Alder, 1862*a* : 144; Alder, 1862*b* : 313, pl. 13, figs 5–7; Alder, 1862*c* : 231–232, pl. 9, figs 5–7; Alder, 1863*a* : 315–316, pl. 14, figs 5–7.
Wrightia arenosa: Allman, 1872 : 300; Bedot, 1925 : 472.
Aselomaris arenosa: Berrill, 1948 : 289; Pennycuick, 1959 : 142, 163–164, pl. 2, fig. 6.

TYPE LOCALITY. Tynemouth and Cullercoats, Northumberland; intertidal, on stones and *Laminaria* holdfasts.

SYNTYPES. **HM** *Spirit* Preserved in two tubes. The first contained three small pieces of rock, one of which bore a small hydroid colony; labelled '*Atractylis arenosa* Alder' and '*Atractylis arenosa*, Tynemouth'. The second tube was labelled '*Atractylis arenosa*, Cullercoats' and '*Atractylis arenosa* Alder', and contained a small amount of dried alga supporting a hydroid colony.

STATUS. Although poorly documented this species seems valid. It is now referred to the genus *Aselomaris* Berrill, 1948.

REMARKS. The availability of the generic names *Atractylis* Wright, 1858, and *Wrightia* Allman, 1872, has been discussed by Totton (1930 : 139), Berrill (1948 : 289) and Pennycuick (1959 : 142). Berrill, having corresponded with W. J. Rees and A. K. Totton (unpublished letters in BMNH), proposed the new name *Aselomaris* in place of *Atractylis*. Totton considered *Aselomaris* a junior synonym of *Bougainvillia* Lesson, 1836.

'Atractylis linearis' Alder, 1862*b*

Hippocrene britannica: Forbes, 1841 : 84, pl. 1, fig. 2a-c.
Bougainvillia britannica: Forbes, 1848 : 62–63, pl. 12, fig. 1a-f.
Atractylis linearis Alder, 1862*b* : 313, pl. 14, figs 1–3; Alder, 1862*c* : 230–231, pl. 10, figs 1–3.
Perigonimus linearis: Allman, 1864*a* : 365.

TYPE LOCALITY. Cullercoats, Northumberland, on *Turritella communis, Astarte danmonia* and other shells from 'deep water'.

SYNTYPES. **HM** *Spirit* Hydroid growths on fragments of *Turritella* shell and on one entire shell of *Astarte*, labelled '*Atractylis linearis* MS. Figured. Cullercoats'.

STATUS. Currently referred to *Bougainvillia britannica* (Forbes, 1841), for example by Edwards (1964) and Russell (1970).

REMARKS. The HM specimens are the whole syntype series.

Eudendrium confertum Alder, 1856*a*

Eudendrium confertum Alder, 1856*a* : 354–355, pl. 12, figs 5–8; Alder, 1857*a* : 103–105, pl. 3, figs 5–8; Alder, 1857*b* : 245; Alder, 1857*c* : 90–91.
Dicoryne stricta Allman, 1859*b* : 369–370.
Dicoryne conferta: Allman, 1861 : 168–171; Millard, 1975 : 101–103, figs 34e-j.

TYPE LOCALITY. Cullercoats, Northumberland (Millard, 1975), on old shells of *Buccinum undatum* and *Neptunea antiqua* from 'deep water'.

MATERIAL. **HM** *Spirit* (Syntypes). Preserved in two tubes and one jar. One tube contained a dried and poorly preserved tangle of hydroid material labelled '*Dicoryne conferta* Alder' and '*Dicoryne conferta*, Mas, Cullercoats'. The second tube contained *D. conferta* on gastropod operculae (probably *Colus* or *Buccinum*), and bore the labels '*Dicoryne conferta* Alder' and '*Dicoryne conferta* var., Cullercoats, with *Farella* [= *Triticella*, Bryozoa] *pedicellata*'. The jar contained *D. conferta* on shell fragments of *Buccinum undatum* and *Colus gracilis* and was labelled '*Dicoryne conferta* Alder' and '*Dicoryne conferta* Alder, Cullercoats'.

BMNH *Spirit* (Non-type) Preserved in two glass jars, both received as part of the A. M. Norman collection. One contained *D. conferta* on small shell fragments, labelled '*Dicoryne conferta*, Cullercoats, Mr Alder', 1912.12.21.153; the second contained *D. conferta* on shells of *Turritella communis*, and was labelled '*Dicoryne conferta*, Cullercoats, Mr Alder', 1912.12.21.154.

STATUS. A valid species referred to the genus *Dicoryne* Allman, 1859*b* (e.g. Hincks, 1868; Millard, 1975).

REMARKS. The HM material is the syntype series. Millard (1975) redescribed the species.

Family EUDENDRIIDAE

Eudendrium capillare Alder, 1856*a*

Eudendrium capillare Alder, 1856*a* : 355–356, pl. 12, figs 9–12; Alder, 1857*a* : 105–106, pl. 3, figs 9–12; Alder, 1857*b* : 245; Alder, 1857*c* : 91; Millard, 1975 : 82, figs 27e-j (syn. *E. parvum* Warren).

TYPE LOCALITY. Embleton Bay, Northumberland; epizoic on the hydroid *Nemertesia ramosa* Lamouroux, 1816; coll. R. Embleton (sic).

MATERIAL. **HM** *Spirit* (Non-type) In two tubes; one containing a dried, fragmented, much branched colony, with two labels—'*Eudendrium capillare* Alder' and '*Eudendrium capillare*, Plymouth'; the other containing several branched fragments, also with two labels—'*Eudendrium capillare* Alder' and '*Eudendrium capillare*, T. Hincks, Cornwall'. *Herbarium* Several branched fragments on one sheet, labelled '*Eudendrium capillare*, deep water, Northumberland'.

STATUS. A valid species (e.g. Millard, 1975).

REMARKS. The original type material, now lost, was in spirit (Alder, 1856*a*). The only remaining Alder specimens from near the type locality are those on the herbarium sheet in the HM. This material might be designated neotype should the need arise.

Family **LAODICEIDAE**

'Campanularia fastigiata' Alder, 1860*a*

Dianaea rotunda Quoy & Gaimard, 1827 : 181–182, pl. 6, figs 1–2.
Campanularia fastigiata Alder, 1860*a* : 73–74, pl. 5, fig. 1; Alder, 1860*b* : 142.
Calycella fastigiata: Hincks, 1868 : 208, pl. 39, figs 3, 3a.
Stegopoma fastigiatum: Levinsen, 1893 : 180, pl. 6, fig. 8; Naumov, 1960 : 315–316, fig. 206; Naumov, 1969 : 341, fig. 206.
Modeeria rotunda: Edwards, 1973 : 573–600.

TYPE LOCALITY. Inner Hauf, Shetland, 'on the stem of *Eudendrium*', dredged by George Barlee, summer 1858.

MATERIAL. **HM** *Spirit* Fragments of *Modeeria rotunda* hydroid in two tubes, one labelled 'Shetland' (holotype), the other 'Hebrides' (non-type).

STATUS. Edwards (1973) considered *Campanularia fastigiata* Alder, 1860*a*, to be the hydroid stage of the medusa *Modeeria rotunda* (Quoy & Gaimard, 1827), the name of which has priority.

REMARKS. The HM Shetlands material is the holotype. *C. fastigiata* has been known as *Stegopoma fastigiatum* for some years. The medusa stage was reared by the late W. J. Rees (unpublished), and the species was referred to the Laodiceidae implicitly on the characters of the medusa by Rees & Rowe (1969). Rees informed colleagues of his identification of the medusa shortly before his unexpected death in 1967. Edwards (1973) noted this, and reared the medusa himself. He confirmed Rees' identification, and gave detailed redescriptions and synonymies.

INCERTAE SEDIS

Campanularia humilis Hincks, 1866

Campanularia humilis Hincks, in Alder, 1862*c* : 239 (nom. nud.).
Cuspidella humilis: Hincks, 1866 : 298; Hincks, 1868 : 209–210, pl. 39, fig. 4; Calder, 1970 : 1512–1513, pl. 3, fig. 2.
?Mitrocomella brownei: Rees & Russell, 1937 : 75–77, figs 9–10.
?Staurophora mertensi: Naumov, 1951 : 747–750 (syn. *C. humilis* Hincks; see remarks).

TYPE LOCALITY. Hincks' (1866, 1868) accounts of the species cited material from Llandudno, North Wales; Whitby, Yorkshire; Northumberland; Shetland; and Connemara; so that the type locality can be taken as the British Isles.

MATERIAL. **HM** *Spirit* Preserved in two tubes, each containing a colony of a '*Cuspidella*' hydroid; the first labelled '*Cuspidella humilis* Hincks' and '*Camp. humilis* + *Laom. lacerata*, Cullercoats'; the second labelled '*Cuspidella humilis* Hincks' and '*Calicella humilis* Hincks, on *Cellularia peachia,* Deep Water; N' (? = Northumberland).

STATUS. Problematical. *C. humilis* is type species of the genus *Cuspidella* Hincks (1866 : 298, by monotypy).

REMARKS. Rees & Russell (1937) reared a hydroid from the medusa *Mitrocomella brownei* (Kramp, 1930) and tentatively referred it to *Cuspidella humilis*. But more than one distinctive medusa species is known to have a 'cuspidella' hydroid, and the hydroids have proved difficult to separate. Thus Naumov (1951) reared such a hydroid from the medusa species *Staurophora mertensi* Brandt, 1838, and considered that it too was identical with *C. humilis*. The problem was reviewed by Calder (1970).

The material listed could be considered type, but no designation is made here pending a better understanding of the life cycles of the species having 'cuspidella' hydroids.

Family **LOVENELLIDAE**

'Lafoea Pygmaea' Alder, in Hincks, 1868

Lafoea pygmaea Alder, in Hincks, 1868 : 205, pl. 40, figs 3, 3a-b.
Calycella pygmaea: Hincks, 1874 : 147.

TYPE LOCALITY. The type series was collected from two widely separated places: Tynemouth, coll. J. Alder; Gouliot Caves, Sark, coll. A. M. Norman.

MATERIAL. **HM** *Spirit* Formerly preserved in three tubes. The first, labelled '*Calicella pygmaea*, on *Thylacium* sp. [= *Stolonica* in part, Tunicata], Gouliot Caves, Sark' and '*Lafoea pygmaea*, Alder', did not contain a hydroid specimen. The second contained a small colony of *Calycella syringa* (Linnaeus, 1767) from which the operculae had been lost, and bore two labels: '*Campanularia pygmaea*, Gouliot Caves, Sark' and '*Lafoea pygmaea* Alder' (holotype). The third tube contained five small pieces of rock and although labelled '*Lafoea pygmaea*, Tynemouth' and '*Lafoea pygmaea,* Alder' contained no hydroid material.

STATUS. Invalid. Hincks (1874 : 147), Bedot (1912 : 315) and Cornelius (1975 : 390) referred *L. pygmaea* to the genus *Calycella*. Jaderholm (1909 : 80–81) and Broch (1918 : 32) went slightly further and indentified it as the species *Calycella syringa*, and we agree.

REMARKS. The material in the second tube was considered type by Cornelius (1975 : 390) and in the absence of other type material can be considered holotype. Bonnevie (1899 : 12) noted that '*L. pygmaea*' resembled *C. syringa* without operculae, but did not propose a synonymy and evidently considered both species valid. The spelling *Calicella* which appears on the label of the first tube relates to a nominal genus in the family Lafoeidae, and is regarded (Cornelius, 1977*b*) a junior synonym of *Lafoea* Lamouroux, 1821.

Family **AEQUORIDAE**

Laomedea acuminata Alder, 1856*b*

Aequorea vitrina Gosse, 1853 : 340, pl. 23; Russell, 1953 : 350–355, pl. 21, figs 2, 4, 5, pl. 32, fig. 3, text-figs 220b, 222–224.
Laomedea acuminata Alder, 1856*b* : 441, pl. 16, figs 5–8.
Campanulina acuminata: Hincks, 1868 : 187–189, pl. 37, figs a-c.

TYPE LOCALITY. Cullercoats, Northumberland, deep water, on 'old shell' of *Neptunea antiqua* (Gastropoda).

TYPE MATERIAL. **HM** *Spirit* Several hydrothecae on broken fargments of calcareous polychaete tubes, labelled 'Cullercoats'.

BMNH *Dry, in box* Small hydroid fragments on barnacle shell, labelled '*Laomedea acuminata* Alder', Northumberland and Durham, pres. J. Alder, 1857.8.3.55.

STATUS. It has been suggested that *Laomedea acuminata* is the hydroid of the medusa *Aequorea vitrina* Gosse, 1853 (Russell, 1953), but the close similarity of *Campanulina paracuminata* Rees, 1938, makes identification uncertain.

REMARKS. The holotype was not found, but the listed material was clearly identified by Alder at some time.

Family **LAFOEIDAE**

'Campanularia gracillima' Alder, 1856*a*

Sertularia dumosa Fleming, 1820 : 83–84.
Campanularia gracillima Alder, 1856*a* : 361, pl. 14, figs 5–6; Alder, 1857*a* : 129–130, pl. 6, figs 5–6; Alder, 1857*b* : 247.
Lafoea dumosa: Cornelius, 1975 : 385–390, fig. 4.

TYPE LOCALITY. 'On shells and zoophytes from deep water, Northumberland coast'.

MATERIAL. **HM** *Herbarium* (Holotype) Much branched colony on herbarium sheet, labelled '*Campanularia gracillima*. Deep water. Northumberland'; figured, Alder, 1856*a*, pl. 14, figs 5–6.

BMNH *Spirit* (Non-type) Two colonies and several fragments in one tube, labelled '*Lafoea gracillima* Alder; Cullercoats; Mr Alder', 1857.8.3.51; designated holotype by Totton (1930 : 159).

STATUS. Referred to *Lafoea fruticosa* (Sars, 1850) by several authors and lately to the older taxon *L. dumosa* (Fleming, 1820) (details in Cornelius, 1975).

REMARKS. Totton (1930 : 159) identified the BMNH material as holotype apparently not knowing about the HM specimen, and his designation is here set aside. Since the HM specimen closely resembles the original illustration in its branching it is more suitable to be regarded holotype. The BMNH specimens are different. The locality of the BMNH specimens, Cullercoats, did not appear in the original description, giving further reason for considering the HM specimen holotype. Cornelius' (1975 : 386, 387) application of paratype status to the HM specimen and of lectotype status to the BMNH material must also be set aside.

'Grammaria ramosa' Alder, 1856*a*

Campanularia abietina Sars, 1850 : 139.
Grammaria ramosa Alder, 1856*a* : 361–362, pl. 14, figs 1–4; Alder, 1857*a* : 130–131, pl. 6, figs 1–4; Alder, 1857*b* : 247; Alder, 1857*c* : 91.
Grammaria abietina: Cornelius, 1975 : 382–385, fig. 3.

TYPE LOCALITY. 'From the deep-water fishing-boats, on the coasts of Northumberland and Durham; rather rare'.

SYNTYPES. **HM** *Herbarium* Branched colony on herbarium sheet, labelled '*Grammaria ramosa*, Northumberland coast'; ?figured, Alder, 1856*a*; pl. 14, fig. 1.

BMNH *Dry in box* Fragment of colony, labelled '*G. ramosa* Alder'; 1857.8.3.52.

STATUS. Regarded conspecific with *Grammaria abietina* (Sars, 1850) by several authors (e.g. Cornelius, 1975).

REMARKS. The HM and BMNH specimens together comprise the syntype series.

Family **HALECIIDAE**

'Halecium filiforme' Alder 1862*b*

Halecium filiforme Alder, 1862*b* : 315; Alder, 1862*c* : 236; Hincks, 1868 : 228.
Halecium muricatum: Cornelius, 1975 : 402–405, fig. 10 (syn. *H. filiforme* Alder).

TYPE LOCALITY. Cullercoats, Northumberland, 'from the fishing boats'.

MATERIAL. **HM** *Spirit* Preserved in two tubes, both found dry. One contained fragments of colonies of *H. muricatum* (Ellis & Solander, 1786) and was labelled '*H. filiforme*, deep water, Northumberland'. The second contained fragments of colonies of *H. sessile* Norman, 1867, and was labelled '*H. filiforme* n. sp., Cullercoats', with the word '*muricatum*' added later by

Alder, presumably when he found later that there was some *H. muricatum* in the tube. *Herbarium* One infertile colony of *H. muricatum*, labelled '*Halecium filiforme*, deep water, Northumberland', designated lectotype by Cornelius (1975 : 405); and three colonies of *H. sessile* on a second sheet, labelled 'Cullercoats' (non-type).

STATUS. Currently referred to *Halecium muricatum* (Ellis & Solander, 1786).

REMARKS. Cornelius (1975) designated the HM herbarium specimen labelled 'deep water, Northumberland' lectotype of *H. filiforme*. It is a large infertile colony of *H. muricatum* (Ellis & Solander, 1786). Hence *H. filiforme* is to be referred to *H. muricatum*. The syntype series of *H. filiforme* was mixed, including specimens of both *H. muricatum* and *H. sessile*, and this was reflected in the description.

Halecium labrosum Alder, 1859*a*

Halecium labrosum Alder, 1859*a* : 354, pl. 13, figs 1–3; Alder, 1859*b* : 126; Alder, 1860*c* : 178–179, pl. 12; Cornelius, 1975 : 396–399, fig. 7.

TYPE LOCALITY. The material on which the original description was based came from 'deep water' off the Northumberland coast (coll. J. Alder), the Moray Firth (coll. 'Macdonald of Elgin') and Shetland (coll. G. Barlee).

SYNTYPES. **HM** *Spirit* Large fertile colony in four pieces, probably ♂; labelled '*Halecium labrosum*, deep water, Northumberland'. *Herbarium* Large colony labelled '*Halecium labrosum*, deep water, Northumberland coast'; ?figured, Alder, 1859*a* : pl. 13, fig. 1.

STATUS. Valid (e.g. Cornelius, 1975).

REMARKS. The original illustration matches the herbarium specimen and might have been prepared from it. Another HM herbarium specimen, labelled '*Halecium labrosum* with capsules, Wick, C. W. Peach Esq.', is not from a type locality and is therefore non-type.

Halecium nanum Alder, 1859*a*

Halecium nanum Alder, 1859*a* : 355, pl. 14, figs 1–4; Alder, 1859*b* : 126; Vervoort, 1968 : 11, 95.

TYPE LOCALITY. Mid-Atlantic (34° 48′N, 34° 25′W); epizoic on Gulf weed, *Sargassum bacciferum* (Turn.) Ag.; coll. William Wright.

HOLOTYPE. **HM** *Spirit* Small ramified colony on *Sargassum* weed, labelled '*Halecium nanum,* Gulf weed'; given to Alder by Joseph Wright of the Hancock Museum.

STATUS. Valid (e.g. Vervoort, 1968).

REMARKS. The labels with the listed specimen give neither collector nor locality. But a jar of *Sargassum* weed with no epizoic hydroid preserved in the HM has the same locality data as the type of *H. nanum*, and it is safe to assume that weed and hydroid were from the same collection. *Sargassum* is a usual substrate for the species. *H. nanum* is the only coelenterate species described by Alder to be based on non-British material.

Family **CAMPANULARIIDAE**

Campanularia hincksii Alder, 1856*a*

Campanularia volubilis var. Hincks, 1853 : 180.
Campanularia hincksii Alder, 1856*a* : 360, pl. 13, fig. 9; Alder, 1856*c* : 347; Alder, 1857*a* : 127–128, pl. 4, fig. 9; Alder, 1857*b* : 246; Alder, 1857*c* : 91; Millard, 1975 : 208, fig. 67, b-e.

TYPE LOCALITY. Northumberland, 'on shells and zoophytes from deep water'.

SYNTYPES. **HM** *Spirit* Several colonies on sertularian hydroids, preserved in two tubes each labelled '*C. hincksii* Alder, deep water'; one of the tubes bearing also a label '*C. verticillata*'.

BMNH *Dry, in box* One colony of *C. hincksii* on *Lafoea dumosa* (Fleming, 1820), labelled '*Camp. hincksii*, Alder' from 'Northumberland and Durham'; pres. J. Alder, 1857.8.3.58.

STATUS. This distinctive species has been widely regarded as valid (e.g. Hincks, 1868; Kramp, 1935; Vervoort, 1946; Millard, 1975).

REMARKS. Alder (1856*a*) included Hincks' (1853) variety of *C. volubilis* in the original synonymy of this species but apparently based his description on new material. The HM and BMNH specimens comprise the syntype series.

Campanularia johnstoni Alder, 1856*a*

Medusa hemisphaerica Linnaeus, 1767 : 1098.
Campanularia johnstoni Alder, 1856*a* : 359–360, pl. 14, fig. 8; Alder, 1857*a* : 126–127, pl. 4, fig. 8; Alder, 1857*b* : 246; Alder, 1857*c* : 91.
Clytia johnstoni: Hincks, 1868 : 143–146, pl. 24, figs 1, 1a; Russell, 1953 : 293, fig. 179.
Phialidium hemisphaericum: Mayer, 1910 : 266–268, figs 140–144; Russell, 1953 : 285–294, pl. 16, fig. 1, pl. 17, fig. 6, text-figs 172–179; Russell, 1970 : 256.
Clytia hemisphaerica: Calder, 1975 : 300–302, fig. 4a-b.

TYPE LOCALITY. Cullercoats, Northumberland; 'on sea-weeds, zoophytes and shells, from between tide-marks to deep water'.

SYNTYPES. **HM** *Spirit* In three tubes. One contained fertile *Clytia hemisphaerica* colonies epizoic on *Abietinaria abietina* (Linnaeus, 1758) and *Flustra* sp. (Bryozoa), with the labels '*Clytia johnstoni* Alder' and '*Campanularia johnstoni*, Cullercoats'. The second contained fertile colonies of *Clytia hemisphaerica* on unidentified algal stipe with labels as on the first tube. The third contained fertile colonies of *Clytia hemisphaerica* on unidentified algal substrate and also bore two labels reading '*Clytia johnstoni* Alder' and '*Campanularia johnstoni* (branched) Cullercoats'. *Herbarium* One colony of *C. hemisphaerica* with several hydrothecae, on *Membranipora* sp. (Bryozoa), labelled '*Campanularia johnstoni* Cullercoats'.

BMNH *Dry, in box* One fertile colony of *C. hemisphaerica* on unidentified algal stipe, labelled '*Campanularia johnstoni* Alder' from 'Northumberland and Durham', pres. J. Alder, 1857.8.3.62.

STATUS. Widely assumed to be the hydroid stage of the medusa *Clytia* (= *Phialidium*) *hemisphaerica* (Linnaeus, 1767); but the identity has not been proved beyond doubt.

REMARKS. The relation between the medusa known as *Phialidium hemisphaericum*, the hydroid *Clytia johnstoni* and other closely related forms from European waters has not been finally worked out (Cornelius, in prep).

'Campanularia raridentata' Alder, in Hincks, 1861

Campanularia raridentata Alder, in Hincks, 1861 : 292; Alder, 1862*b* : 315–316, pl. 14, fig. 5; Alder, 1862*c* : 238–239, pl. 10, fig. 5.
Campanularia ?raridentata: Hincks, 1868 : 176–177, pl. 26, figs 2, 2a; Rees & Thursfield, 1965 : 92–93.
Clytia hemisphaerica: Rees & Thursfield, 1965 : 95–96.

TYPE LOCALITY. Cullercoats, Northumberland; epizoic on other hydroids (Alder, 1862*b*).

HOLOTYPE. **HM** *Spirit* One small infertile colony resembling the original illustration, epizoic on small branched colony of *Hartlaubella gelatinosa* (Pallas, 1766); '*Campanularia raridentata* Alder' and '*Camp. raridentata* on *Laomedea*, Cullercoats'.

STATUS. Referred to *Clytia hemisphaerica* (Linnaeus, 1767). *C. raridentata* sensu Alder, 1862*b*, was considered 'one of the many forms of *Clytia hemisphaerica*' by Rees & Thursfield (1965); while Alder (1862*b*) himself separated it from *C. hemisphaerica* (as *C. johnstoni* Alder, 1856*a*) only on its smaller size.

REMARKS. The HM specimen is the holotype. We confirm that it is a young colony of *Clytia hemisphaerica* auct., but the remarks made under the previous species should be noted. '*Campanularia raridentata*' was wrongly ascribed to 'Alder, 1857' by Rees & Thursfield (1965 : 92).

Laomedea flexuosa Alder, 1857*a*

Laomedea flexuosa Hincks, in Alder, 1856*b* : 440 (nom. nud.); Alder, 1857*a* : 122–123; Alder, 1857*d* : 32–33; Hincks, in Allman, 1859*a* : 137; Hincks, 1861 : 260; Cornelius, in prep.
Campanularia flexuosa: Hincks, 1868 : 168–170, pl. 33.

TYPE LOCALITY. British Isles.

MATERIAL. **HM** *Spirit* (Syntypes). Specimens in three tubes. The first contained several small colonies, one with several well preserved ♀ gonothecae; labelled '*Campanularia flexuosa* Hincks' and '*Laomedea flexuosa*, Tenby'. The second contained several colonies, one a fertile ♀; labelled '*Campanularia flexuosa* Hincks' and '*Laomedea flexuosa*, Tynemouth, Northumberland'. The third contained several colonies, some fertile ♀, on two pieces of *Ascophyllum nodosum* (L.) Le Jol.; labelled '*Campanularia flexuosa* Hincks' and '*Laomedea flexuosa*, Loc. nr. Lerwick, Shetd?'. *Dry* (Non-types). Stolon growths on 7 rock fragments and 4 valves of young mussels; labelled '*Campanularia flexuosa* Hincks' and, by Alder, '*Laomedea flexuosa*; *Coryne ramosa*; Tynemouth'; confirmation of identifications not possible.

BMNH *Dry, in box* Two fertile colonies; labelled '*Laomedea flexuosa*, Hincks (Alder), Tenby', probably by Alder; 1857.8.3.54.

STATUS. A valid and well known species.

REMARKS. The name *flexuosa* was introduced by Alder (1856*b*) without a description. Although he cited Johnston's (1847) description of '*Laomedea gelatinosa* var. *α*' that in turn was not based on material or other indication. Hence Alder's (1856*b*) introduction of *flexuosa* cannot be accepted. But he was soon to provide adequate description (Alder, 1857*a*, *d*), so validating this widely used name. Allman (1859*a*) was next to use the name, and like Alder (1856*b*) ascribed it to 'Hincks, in MS'. Some years passed before the name was published by Hincks (1861) himself, however; and several more years before the species was illustrated under its own name by any author (Hincks, 1868).

The syntype series comprises material from England, Scotland and Wales and it is appropriate to restrict the type locality to the British Isles.

Laomedea neglecta Alder, 1856*b*

Laomedea neglecta Alder, 1856*b* : 440, pl. 16, figs 1–2; Alder, 1857*a* : 123, pl. 5, figs 1–2; Alder, 1857*b* : 246; Alder, 1857*d* : 33–34, pl. 3, figs 1–2; Hincks, 1868 : 171–172, pl. 30, fig. 2; Cornelius, in prep.

TYPE LOCALITY. Cullercoats and Tynemouth, Northumberland; intertidal, 'on undersides of stones'.

MATERIAL. **HM** *Spirit* Preserved in two tubes and a jar. The first tube contained five dry fragments of rock, one bearing a hydrocaulus. This was mounted in balsam and identified as *Laomedea flexuosa* Alder, 1857*a*, and was evidently not part of the type series. The tube was labelled '*Campanularia neglecta* Alder' and, by Alder, '*Laomedea neglecta*, Cullercoats'. The second tube contained four hydrocauli on a piece of algal stipe, probably representing a single colony. These also were mounted in balsam, but identified as *L. neglecta*. The labels read '*Campanularia neglecta* Alder' and '*Laomedea neglecta*, Roach River, Ex' [= Essex]. Although locality and substrate indicate that this material was not part of the syntype series, in the absence of any of the syntype material this colony is designated neotype. The third container, a jar, contained 22 small rock fragments but only one bore a hydroid colony. There were no hydrothecae but the hydrocaulus was more robust than in *L. neglecta*, and the colony was probably *L. flexuosa*. The labels read '*Campanularia neglecta* Alder' and '*Laomedea neglecta*, Cullercoats'. It would be confusing if this material, or that in the first tube, were regarded type of *L. neglecta* since that name would then attach to *L. flexuosa* auct., a widely known species. Designating the material in the second tube neotype avoids this problem.

BMNH *Dry, in box* Minute stolon fragments on two small pieces of rock; labelled '*Laomedea neglecta* Alder'; pres. J. Alder; 1857.8.3.63. Not identifiable as type material.

STATUS. Widely regarded as valid (e.g. Vervoort, 1946; Cornelius, in prep.). Although not often reported from British waters the species is hard to find and may prove commoner than the records suggest.

REMARKS. The fine cusps characteristic of the hydrothecal rim in this species are clearly visible in parts of the neotype material.

Laomedea loveni Allman, 1859*a*

Laomedea loveni Allman, 1859*a* : 138–140.
Gonothyraea loveni: Hincks, 1868 : 181–183, pl. 25, fig. 2.

REMARKS. Although this species was originally described in the eighteenth century by Ellis (1756), for the next hundred years it was confused with both the *Obelia* spp. and *Laomedea flexuosa* (details in Allman, 1859*a*; Hincks, 1868; Cornelius, 1977*a*). Allman (1859*a*) wrote that Alder had told him (in litt.) that the present species was 'distinct, though not yet discriminated'; and Alder was clearly among the first to make this discovery. But the species was named by Allman.

In the previous year Wright (1858, repeated in 1859), apparently independently, reported that *G. loveni* was distinct. But he too did not provide a specific name. It might now be difficult to establish whether Alder or Wright was the first to regard *G. loveni* as distinct, and whether or not they worked independently.

We have not located type material. The spelling *Gonothyrea* has often been used but is incorrect (details in Cornelius, in prep.).

Family **SERTULARIIDAE**

Sertularia tenella Alder, 1856*a*

Sertularia rugosa var. Johnston, 1847 : 63–64, pl. 10, figs 4–6.
Sertularia tenella Alder, 1856*a* : 357–358, pl. 13, figs 3–6 (nom. nov. for *S. rugosa* var. Johnston); Alder, 1857*a* : 113–114, pl. 4, figs 3–6; Alder, 1857*b* : 246; Alder, 1857*c* : 91.
Sertularella tenella: Hincks, 1868 : 242–243, pl. 47, figs 3, 3a-c; Cornelius, 1979 : 292–294, fig. 24.

TYPE LOCALITY. None was given by Alder but it can be restricted to the coastal waters of Northumberland. The original description was based on colonies epizoic on *Hydrallmania falcata* (Linnaeus, 1758), but these colonies could not be found.

SYNTYPES. **HM** *Herbarium* Several colonies on *Abietinaria abietina* (Linnaeus, 1758), labelled '*Sertularia tenella*, Cullercoats'.

BMNH *Dry, in box* Two hydrocauli, labelled '*Sertularia tenella* Alder'; Northumberland, pres. J. Alder, 1857.8.3.49.

STATUS. The distinction from *Sertularella rugosa* (Linnaeus, 1758) is doubtful but at present *S. tenella* is accepted (Cornelius, 1979).

REMARKS. The originally illustrated specimen of *S. tenella*, epizoic on *Hydrallmania falcata*, was not found. Hence the HM and BMNH material listed here represents an incomplete syntype series. Nutting (1904 : 84) identified the HM material as type but the BMNH specimens also are part of the syntype series.

Sertularia tricuspidata Alder, 1856*a*

Sertularia tricuspidata Alder, 1856*a* : 356–357, pl. 13, figs 1–2; Alder, 1857*a* : 111–112, pl. 4, figs 1–2; Alder, 1857*b* : 245–246; Alder, 1857*c* : 91.
Symplectoscyphus tricuspidatus: Stechow, 1923 : 173; Cornelius, 1979 : 301–304, fig. 28.

TYPE LOCALITY. 'On zoophytes from deep water on the Northumberland coast'.

SYNTYPES. **HM** *Spirit* Several fertile colonies in one tube, bearing two labels: '*Sertularella tricuspidata* Alder' and '*Sertularia tricuspidata*, with ovicapsules'. *Herbarium* Single colony labelled '*Sertularia tricuspidata* var., Northumberland coast, from the deep water boats'; several colonies on 150 mm colony of *Abietinaria abietina* (Linnaeus, 1758), labelled '*Sertularia tricuspidata*, on *Sertularia abietina*, deep water, Northumbd'; probably syntypes; four colonies, one fragmented, on third herbarium sheet, labelled '*Sertularia tricuspidata*, deep water, Northumberland coast'.

BMNH *Herbarium* Four colonies on one sheet, labelled '*Sertularia tricuspidata* Alder, Northumberland coast'; 1919.4.5.6.

STATUS. A valid species, currently referred to the genus *Symplectoscyphus* Marktanner-Turneretscher, 1890 (see Cornelius, 1979).

REMARKS. Nutting (1904 : 100–102) identified the HM material as type, but that in the BMNH is also part of the syntype series. The species was redescribed by Cornelius (1979).

Family **PLUMULARIIDAE**

Plumularia halecioides Alder, 1859*a*

Plumularia halecioides Alder, 1859*a* : 353, pl. 12, figs 1–4; Alder, 1859*b* : 126; Alder, 1860*c* : 177–178, pl. 11a.
Ventromma halecioides: Stechow, 1923 : 220.

TYPE LOCALITY. Cullercoats, Northumberland, 'near low water mark', on stones, summers of 1857 & 1858 (coll. J. Alder); and Roker, Durham (coll. A. Hancock).

TYPE MATERIAL. **HM** *Spirit* In two tubes, one with three fragmented fertile colonies, the second containing several fertile fragments; both tubes labelled '*Plumularia halecioides*, Cullercoats'. *Herbarium* Six hydrocauli on a herbarium sheet, labelled '*Plumularia halecioides*, Cullercoats'.

BMNH *Spirit* One small infertile colony on rock, given by Alder to A. M. Norman, Cullercoats, 1912.12.21.475.

STATUS. A valid species. *P. halecioides* is type species of the genus *Ventromma* Stechow, 1923 : 219 (by original designation). Several authors have placed the species in that genus (Leloup, 1935; Bruce *et al.*, 1963; Rees & Thursfield, 1965; Mammen, 1967), but others have retained it in *Plumularia* Lamarck, 1816 (Naumov, 1960, 1969; van Gemerden-Hoogeveen, 1965; Vervoort, 1967). Mammen (1967) discussed the problem and upheld the separation, based on the presence of a supracalycine nematophore in *Ventromma* but not in *Plumularia*. We provisionally agree, and the present species should be known as *Ventromma halecioides*; but we cannot agree with Mammen that *Ventromma* differs enough to be placed in a distinct subfamily.

REMARKS. It is not clear when Alder saw the listed material. Therefore, it is unclear whether the specimens should be regarded as syntypes or, having been identified after the first description was published, are merely available to be designated neotypes should the need arise. The absence of material from the Roker locality suggests that at least some of the original syntype series might still be found.

Hydroid type material in the Hancock Museum of authors other than Alder

It is evident from the collection of hydroids in the Hancock Museum that Alder received hydroid material from most of the prominent hydroid students of his time. Some of these fragments may be syntypes of the species they described. This material is listed below.

Campanularia angulata Hincks, 1861

Material cited in the original description was collected from Torbay and the Isle of Man. The HM collection includes a colony on *Zostera* L. (eel grass), in spirit, labelled '*Laomedea angulata*, Ramsey, Isle of Man, Revd. T. Hincks', and this is almost certainly part of the syntype series. The species has been revised by Cornelius (in prep.).

Aglaophenia tubulifera (Hincks, 1861)

The type locality is 'deep water, coast of Cornwall' (Hincks, 1861; Svoboda, 1979). The HM collection includes a stem with a few side branches remaining, in spirit, labelled '*Plumularia tubulifera*, Cornwall, Revd. T. Hincks'. Another, darker, specimen in the same tube is presumably that referred to by an additional label 'dark specn. Connemara'. Undoubted type material of *A. tubulifera* is held in the BMNH. The species has been revised by Svoboda (1979).

'Sertularia gracilis' Hassall, 1848

The type series came from Brighton and Ramsgate, SE England (Hassall & Coppin, 1852; Cornelius, 1979). What remains of it is divided between HM and BMNH. That in the HM comprises two colonies in spirit and a herbarium specimen. Those in spirit are labelled '*Sertularia gracilis*, Brighton' by Alder, with the word 'Guernsey' added by someone else; on alga, probably *Chondrus crispus* Stackh. (det. J. H. Price). The herbarium specimen is a dense growth on *Chondrus*, labelled 'Brighton, J. Coppin Esq.', the collector's name being feint, at lower right.

Hassall (1848) gave the 'average diameter' of the hydrothecae as 1/316 inches (= 0·19 mm), and of the gonothecae as 1/136 inches (= 0·08 mm). We measured part of the BMNH spirit material (listed in Cornelius, 1979) and confirm these measurements.

The species is now referred to *Sertularia distans* Lamouroux, 1816 (revision in Cornelius, 1979).

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A new genus of toad (Anura: Bufonidae) from the Republic of South Africa with remarks on its relationships

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Hewitt (1926) described two small species of toads from the Cape Region of South Africa. He believed them to be closely related and distinguished them on the basis of size and the presence of an ear in the larger species, *Bufo tradouwi*. Both *B. tradouwi* and the smaller species, *B. rosei*, occur in the Cape Folded Mountain Belt, *tradouwi* being first described from the Swellendam Mountains and the Tradouw Pass at 1067–1676 m and *rosei* from the plateau above Muizenberg Mountain in the Cape Peninsula at 335 m, about 200 km to the west. In 1929 Power & Rose gave an account of the habits and life history of *rosei*, including a description of the eggs and tadpole. They stated that they believed *rosei* to be confined to the Cape Peninsula and quoted the vertical distribution of the species as 244 m at the southern tip of the Cape Peninsula, to 1006 m on Table Mountain. They referred to a juvenile collected at a band of shale at 1067 m in the Cedarberg Mountains (about 200 kms NNE of the Peninsula) as resembling *rosei* except for an indistinct tympanum being present and suggested that it may 'be a link between *B. rosei* and *B. tradouwi*'.

No further published reports appeared on these taxa until in 1964 Poynton synonymized them, believing that intraspecific variation could account for the loss of ear elements in *rosei*. Tandy & Keith (1972) resurrected *tradouwi* and, along with *B. gariepensis* Smith, *B. inyangae* Poynton and *B. amatolica* Hewitt placed it with the *angusticeps* Smith group, a group restricted to extreme Southern Africa and distinguished by them as 'small to medium sized toads having smooth skins, hypertrophied testes with a peculiar biochemical effect on eggs of other species when squashed and used in artificial crosses'. They placed *B. rosei* in a separate group but mentioned that its smooth skin and hypertrophied testes and its detailed anatomy and distribution in relict populations on mountain summits of the Cape Peninsula and Cape Folded Mountains suggest a closer affinity to the *angusticeps* group than to the earless *Bufo taitanus* Peters which they felt bore a superficial resemblance to *rosei*. Their reference to its detailed anatomy was not further explained nor did they elaborate on its resemblance to *B. taitanus*. The only published work on the osteology of *B. rosei* is one short paragraph (Martin, 1972) in which three dermal skull elements are described.

Like Tandy & Keith I could not accept Poynton's synonymising *tradouwi* with a species that in lacking middle ear elements has undoubtedly different ecological requirements, a different behavioural pattern as well as a more derived morphology. As part of my ongoing research into the comparative morphology of the osteocranium, vertebrae and myology of African bufonids material identified as *rosei* and *tradouwi* was examined. Results demonstrate that *tradouwi* is indeed distinct from *rosei*, that they are clearly distinguishable from each other by both external and internal morphological characters and that they are allopatric montane species with different but perhaps overlapping vertical distributions. They are separated geographically by the deep gap, the Nuwe Kloof, which divides the Bains Kloof Mountains from the Great Winterhoek Mountains, and by the Valley of the Breede River which stretches from the Tulbagh/Worcester valley southeastwards to Witsand on the south coast. *Bufo rosei* is confined to the area south west of this barrier, *Bufo tradouwi* to the Cape Folded Mountains to the north and east. The suite of characters possessed by *tradouwi* and *rosei* suggests that these Cape taxa are early derivatives from a stock that also gave rise to

Bull. Br. Mus. nat. Hist. (Zool.) **39** (5) : 293–298 Issued 18 December 1980

Nectophrynoides and the Cameroun montane forest genera. Recognition of a new genus to accommodate *tradouwi* and *rosei* is proposed.

CAPENSIBUFO gen. nov.

TYPE SPECIES. *Bufo tradouwi* Hewitt 1926 : 486.

CONTENT. Two species, *Bufo rosei* Hewitt and *B. tradouwi* Hewitt, found in the South-western Cape, Republic of South Africa.

DIAGNOSIS. (1) Small bufonids with rather smooth soft skin and scattered blister-like ridges and warts on the back and flanks. (2) Paratoids distinct, usually pear-shaped in *tradouwi* and inverted pear-shaped in *rosei*. (3) Ear present (*tradouwi*) or absent (*rosei*). (4) Toes without web, subarticular tubercles moderately developed, distal ones tending to divide, terminal phalanges simple, not expanded. (5) Tarsal fold absent. (6) A large subcircular, corrugated area post abdominally. (7) Vent ventral in sexually mature males of *rosei*, dorsal and terminal in females of both species and in male *tradouwi*. (8) Spinules in an axillary patch in breeding male *tradouwi*; nuptial pads on first and second fingers in adult males of both species. (9) Testes slender, cream, not hypertrophied in *tradouwi* 1/6 snout-vent length; broadly oval, twice as long as broad, heavily pigmented in *rosei* 1/4 snout to vent length. (10) Eggs pigmented, large (diameter 2·0 mm), clutches small (< 100). Head and body length of gravid females 27·0–33·6 mm (*tradouwi*) 29·0–32·5 mm (*rosei*). (11) Adult males of *tradouwi* larger than females (33·1–37·0 mm), smaller than females in *rosei* (21·3–27·8 mm). (12)

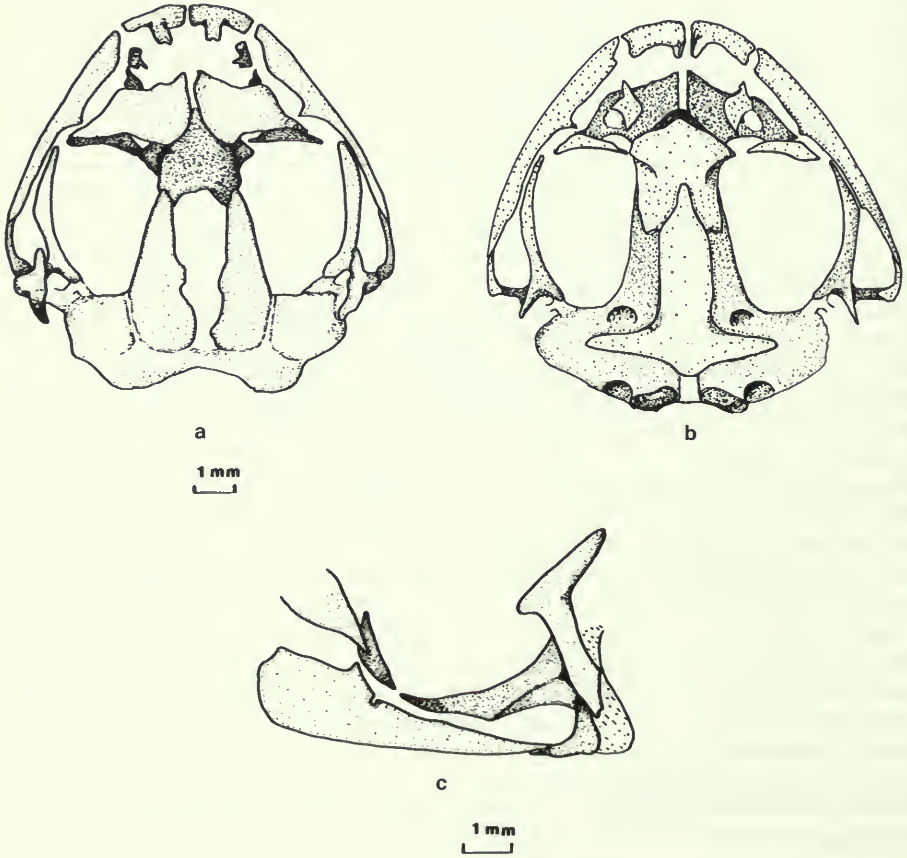

Fig. 1 Skull of *Capensibufo tradouwi*. (a) dorsal, (b) ventral, (c) lateral.

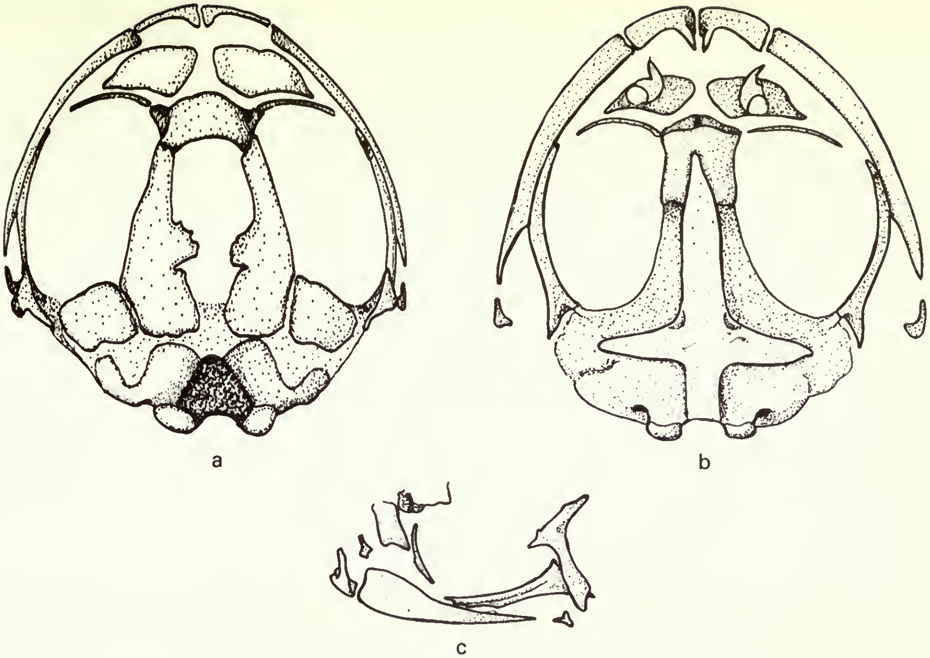

Fig. 2 Skull of *Capensibufo rosei*. (a), dorsal, (b) ventral, (c) lateral.

Omosternum present. (13) Adductor longus muscle present and long. (14) Tensor fasciae latae short, arises from distal 1/4 of ilium and inserts on cruralis muscle at mid thigh (*tradouwi*) or proximal 1/3–1/4 of thigh (*rosei*). (15) Iliacus externus muscle bulky, its origin on distal 1/2 of ilium (*tradouwi*) or moderately well developed and with a more extensive origin (*rosei*). (16) Large frontoparietal fontanelle. (17) Open occipital canal. (18) Squamosal shaft fully ossified. (19) Otic ramus narrow and long, an otic plate barely discernible. (20) Zygomatic ramus short. (21) Parasphenoid flat, devoid of keels, the cultriform process in *tradouwi* squat but tapering anteriorly where overlapped by sphenethmoid, in *rosei* longer and considerably slimmer. (22) Quadratojugal varies interspecifically; in *tradouwi* it meets both the quadrate and the maxilla, is narrowly overlapped by the latter and borders distal 1/2 of pterygoid fossa while in *rosei* it is vestigial and contacts neither the quadrate nor the maxilla. (23) Palatine reduced in both species, occasionally failing to meet sphenethmoid, separated from both the maxilla and pterygoid. (24) A large dorsal sphenethmoid exposure. (25) Nasals separated medially. (26) Medial ramus of pterygoid short, well separated from parasphenoid ala. (27) Preorbital processes well developed but not overlapping in anterior/posterior plane (*tradouwi*) or absent (*rosei*). (28) Occipital condyles/cervical cotyles narrowly separated (*tradouwi*) or widely separated (*rosei*). (29) Eight presacral vertebrae. (30) Sacrococcygeal articulation bicondylar (*tradouwi*) or with a trend in *rosei* towards monocondyly.

ETYMOLOGY OF GENERIC NAME

Capensis: adjective relating to the Cape of Good Hope and to the phytochorological subdivision of the southern and western Cape Province.
Bufo: Latin for toad.

ECOLOGY AND HABITAT

The Capensis, the vegetation zone in which both *rosei* and *tradouwi* occur, has a distinctive and diverse flora and fauna with a high speciation rate. The dominant vegetation type is Cape fynbos, a term Taylor (1978) defines as being characterised by three elements—restioid, ericoid and proteoid—with rarely one species dominant. J. C. Greig (personal communication) believes that both species of *Capensibufo* occupy similar habitats and

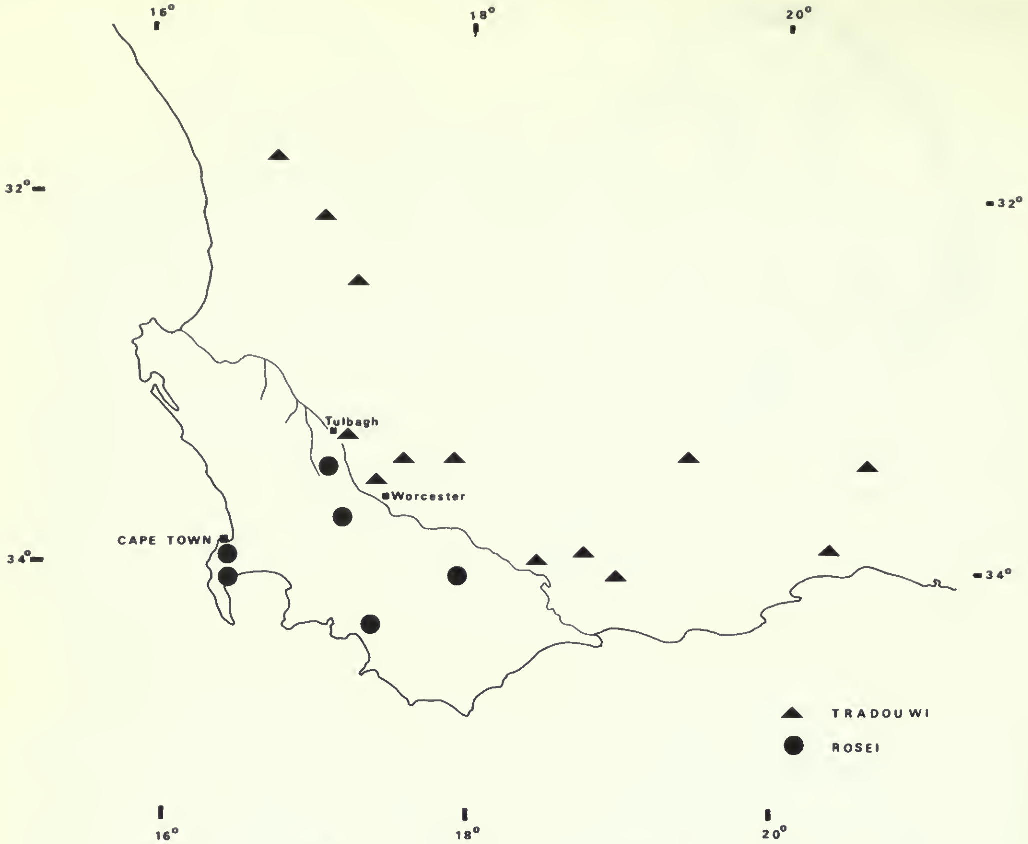

Fig. 3 Locality records of *Capensibufo*.

describes a collecting area for *rosei* in the Klein River Mountains as a seepage marsh (adults with spawn obtained in July) and on a footpath where the vegetation is ericoid-restioid mountain fynbos with perennial seepage.

Power & Rose (1929) describe the breeding pool of *rosei* as an ephemeral puddle 4 × 2 ft and 4 inches deep, devoid of vegetation but with a muddy base. J. Visser (personal communication) describes the breeding pools as being rock pools of approximately 2 × 1 ft but because he did not distinguish *tradouwi* from *rosei* in the field and was unaware that the '*rosei*' material he collected at Pakhuis is actually *tradouwi* (specimens examined in present study) there is some uncertainty whether both species spawn in pools of similar size and substrate.

Remarks on likely origin of Capensibufo and its relationships

Taylor (1978) points out that the Capensis is so distinct that it is generally recognised as a floral kingdom on its own. Seven families of plants are endemic to the Capensis and he quotes Good (1974) as claiming that the Capensis may have the highest endemism in the world. The distinctiveness of both its flora and fauna is well documented and is thought to be attributable to its great age, its isolation spanning over 100 million years and its ability to survive climatic changes. Axelrod & Raven (1978) suggest that two major episodes of speciation took place in southern Africa, one in the Miocene and the second during the climatic fluctuations in the Pliocene and Pleistocene when the mountains were raised around the rim of South Africa. What is less clear is whether the ancestors of the Capensis herpetofauna migrated southwards from the montane forests of Central Africa, after Africa became isolated from Gondwanaland and drifted northwards, or whether they originated in South Africa as fragments of an ancient group that once was distributed throughout S.

America, Australia, Antarctica, India and Madagascar. I believe an austral derivation for the African members of the family Bufonidae accords more satisfactorily with the evidence that has accrued from my study of their osteology and some myological features, most of the southern African bufonids having a smaller number of shared derived character states than any Central African ones.

No present day African species of *Bufo* seems to be closely related to *Capensibufo*. Examination of 80% of the taxa currently recognised reveals that none has a rod-like otic ramus with only an incipient dorsal plate, none has an omosternum, none has marked reduction of the quadratojugal, none has reduced palatines, none has a frontoparietal fontanelle, none has a long iliacus externus muscle and none displays a trend towards a modified arciferal condition in the pectoral girdle. But some or all of these characteristics of *Capensibufo* are met with in *Nectophryne, Laurentophryne, Wolterstorffina, Werneria, Nectophrynoides* and *Didynamipus* (Grandison, 1978 and in press), genera that I believe are derived from a common ancestor. It appears logical on the basis of an analysis of 24 osteological, myological and external characters which were selected as being potentially useful indicators of evolutionary trends to regard *Capensibufo* as an advanced derivate from this ancestor which while retaining the adductor longus muscle and the omosternum of the ancestor has evolved in isolation a number of derived character states chiefly through reduction of cranial elements. Further discussion of the relationships of *Capensibufo* and the analysis of characters is given in the forthcoming paper on *Didynamipus* (Grandison, in press).

Acknowledgements

For his interest and generous help in supplying material and making available his personal observations on the niche occupied by *C. rosei* I extend sincere thanks to Mr John Greig (Jonkershoek Nature Conservation Station, Stellenbosch). Also gratefully acknowledged is the asistance given by Dr W. Branch (Port Elizabeth Museum) who aided the project in many ways and by Dr G. McLachlan (South African Museum) who provided most of the *tradouwi* study material. Dr W. Haacke (Transvaal Museum), Mr Hymen Marx (Field Museum of Natural History), Mr John Visser (Cape Town) and Dr E. E. Williams (Museum of Comparative Zoology) generously lent or donated specimens. Cordial thanks are also extended to my colleagues Dr P. H. Greenwood, whose knowledge of the Cape I tapped, Dr W. T. Stearn, who proposed the generic name and supplied the etymology and Mr B. T. Clarke with whom I have enjoyed lively discussions on phylogenetic inference and who skillfully prepared the stained and cleared specimens.

Capensibufo Study Material

rosei: 94 examples including 2 dry skeletons and 4 stained and cleared preparations. BM 1903.11.10.3–4, BM 1905.10.18.30, BM 1925.12.18.139–148, BM 1978.977–978, BM 1978.2237–2238, FMNH 187207–187265, FMNH 82692, FMNH 130946–130951, FMNH 166527, MCZ 10914–10916, PEM 101–102, SAM 19435(2), TM 26603, TM 26611, TM 52624.

tradouwi: 27 examples including 1 stained and cleared preparation. PEM 306, MCZ 98780–98781, SAM 14233, SAM 17389 (3), SAM 17854, SAM 18017, SAM 18188–18189, SAM 18192 (2), SAM 18303 (2), SAM 18341 (6), SAM 18345, SAM 18523, SAM 18783 (2), SAM 19439, SAM 20516–20517, SAM 43813, TM 52616, TM 52627–8.

Abbreviations used

BM	British Museum (Natural History)
FMNH	Field Museum of Natural History
MCZ	Museum of Comparative Zoology
PEM	Port Elizabeth Museum
SAM	South African Museum
TM	Transvaal Museum

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Aspects of breeding morphology in *Mertensophryne micranotis* (Anura: Bufonidae): secondary sexual characters, eggs and tadpole

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Introduction

A few years ago while examining the holotype and paratype of the East African dwarf toad *Mertensophryne micranotis* (Loveridge), series of tiny, conical, unpigmented spines, some of which appeared to be inward curving, were noticed on the puckered rim and inner surface of the vent in the male paratype. Loveridge (1925) described the specimen, which measured 22 mm in snout to vent length, as having been taken *in coitu* with the slightly larger (23 mm) female holotype. However he made no mention of these curious vent structures. Nor did he describe the cluster of heavily cornified spines on the male's thumbs which are quite unlike the thumb pads of any other African bufonid, except the Mount Nimba viviparous toads, *Nectophrynoides liberiensis* Xavier and *N. occidentalis* Angel. The vent of other adult male *micranotis* available to the author at that time was not similarly modified.

Because the vent skin of the male paratype had been damaged by having had a pin driven through it and because there was a slight possibility of the spines being of no sexual significance a report of this author's observation was delayed pending the collection of additional sexually mature individuals.

Recently further material from forested coastal areas of Tanzania and Kenya have been made available for study. The Kenyan material comprises adults and larvae obtained from crevices in rotten trees 1·5 m from the forest floor and further adults from *Achatina* shells. The collector was attracted to the tree hole by faint high pitched squeaking (A. Duff-Mackay, pers. comm.). Although the material now available contains several males with fully developed thumb asperities only two of the recently acquired specimens also have spines on the vent. One of the two males was found with a gravid female in a tree cavity on 18 May 1971. It is conjectured that these vent structures probably develop only at the peak of spermatogenesis and regress shortly after mating and while the thumb asperities are still cornified. If this is so, then it is reasonable to assume that they function as a coupling device, perhaps enabling the male to maintain a tenacious grip on the female's vent during mating. Because a coupling device would be superfluous in species practising external fertilisation its occurrence in *micranotis* could indicate that the eggs in this species are internally fertilised.

By dissecting the cloacal tube and with the aid of interference contrast microscopy the spines were revealed as being restricted to the ridges of the puckers of the vent; none lies in the furrows. There appear to be approximately three tiers of spines, the outermost on the rim of the vent, the others internally at the entrance to the cloacal tube. All are orientated towards the lumen but directed somewhat posteriorly, Fig. 2.

It is suggested that in amplexus the male's spines slot into the furrows of the corrugations of the female's orifice. If they are supplied with a capillary network they may become erectile during amplexus, thus increasing the male's penetration of the female's vent, as well as his area of attachment to his mate. No pores, papillae or setae or other external structural modification suggesting a sensory function were detected by stereoscanning the spines. The presence, postion and orientation of the spines are interpreted as a modification for ensuring a close fastening of the vents of the two sexes during insemination and preventing loss of sperm.

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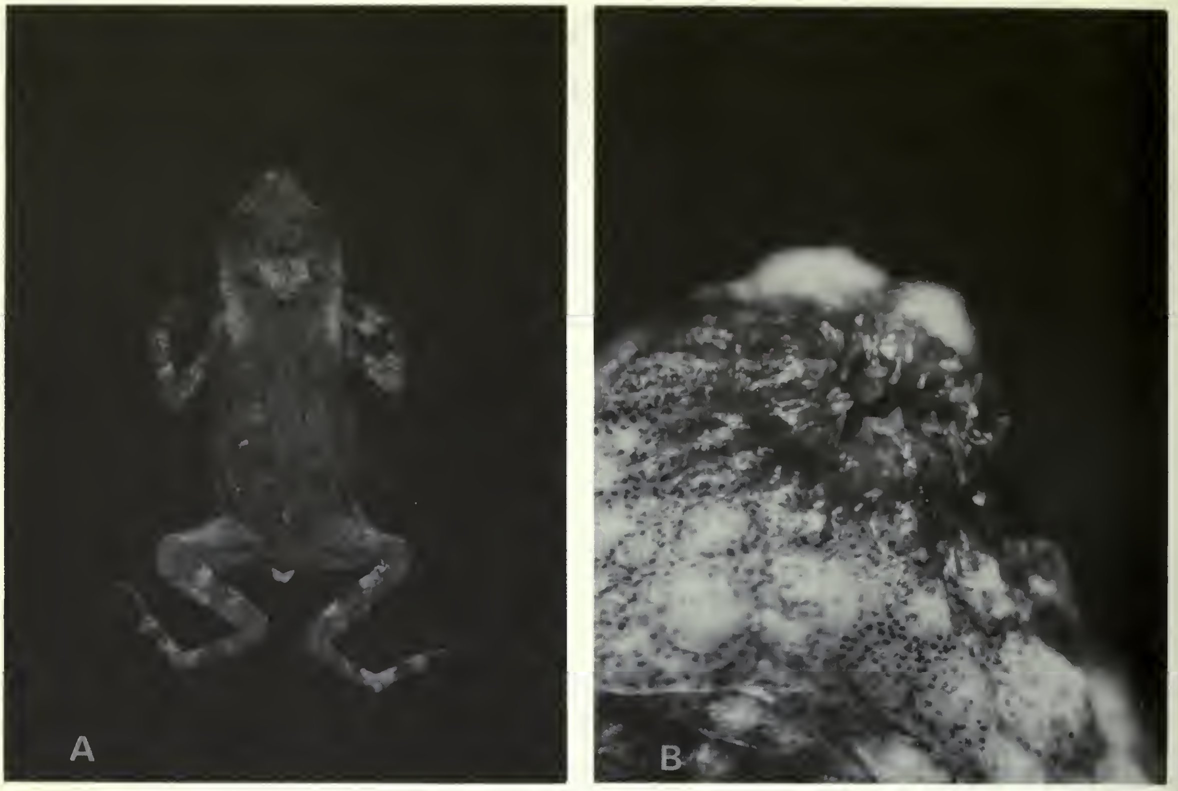

Fig. 1 *Mertensophryne micranotis:* A, dorsal view of subadult A/1270/1 × 3; B, spines surrounding the vent of a sexually mature male A/1150/2 × 5.

Eggs and internal fertilisation

In an attempt to test the hypothesis of internal fertilisation, eggs of two gravid females, one of which (the holotype) was taken in amplexus, were examined but no evidence of cell division was found. In the case of the holotype, such evidence would be unlikely for if sperm had entered the female the interval between the event and the female being killed and preserved could have been insufficient for the sperm to have reached the ova. The non-typical female may not have mated or, if inseminated, its eggs like those of the holotype may not have had time to undergo cell division. The eggs on one side of one female were removed, measured and counted. They are in three size classes. The largest class (av. diam. 1·8 mm) are lightly pigmented at the animal pole and number 16, the middle class (av. diam. 1·0 mm) are more heavily pigmented and number nine. The smallest ova are uniform white and only 0·4 mm in diameter. The total complement of eggs is estimated at 76.

The eggs and amplexus in other African bufonids

Only five other species of African bufonids have been found to contain clutches of less than 100 pigmented ova. Schmidt & Inger (1959) quote egg counts of 31 and 35 large ova in two females of their new species *Bufo melanopleura*, which measured 22·2 mm SVL and 22·7 mm SVL respectively. In addition each ovary had as many small immature ova as mature ones. Although Tandy & Keith (1972) report the clutch size in *Stephopaedes anotis* (Boulenger) as 22 and attribute this count to Poynton (1964), in fact Poynton cites 85.

Novak & Robinson (1975) provide data on the average clutch size and egg diameter for a number of species of *Bufo*, including a few African ones, but repeat the error made by Power

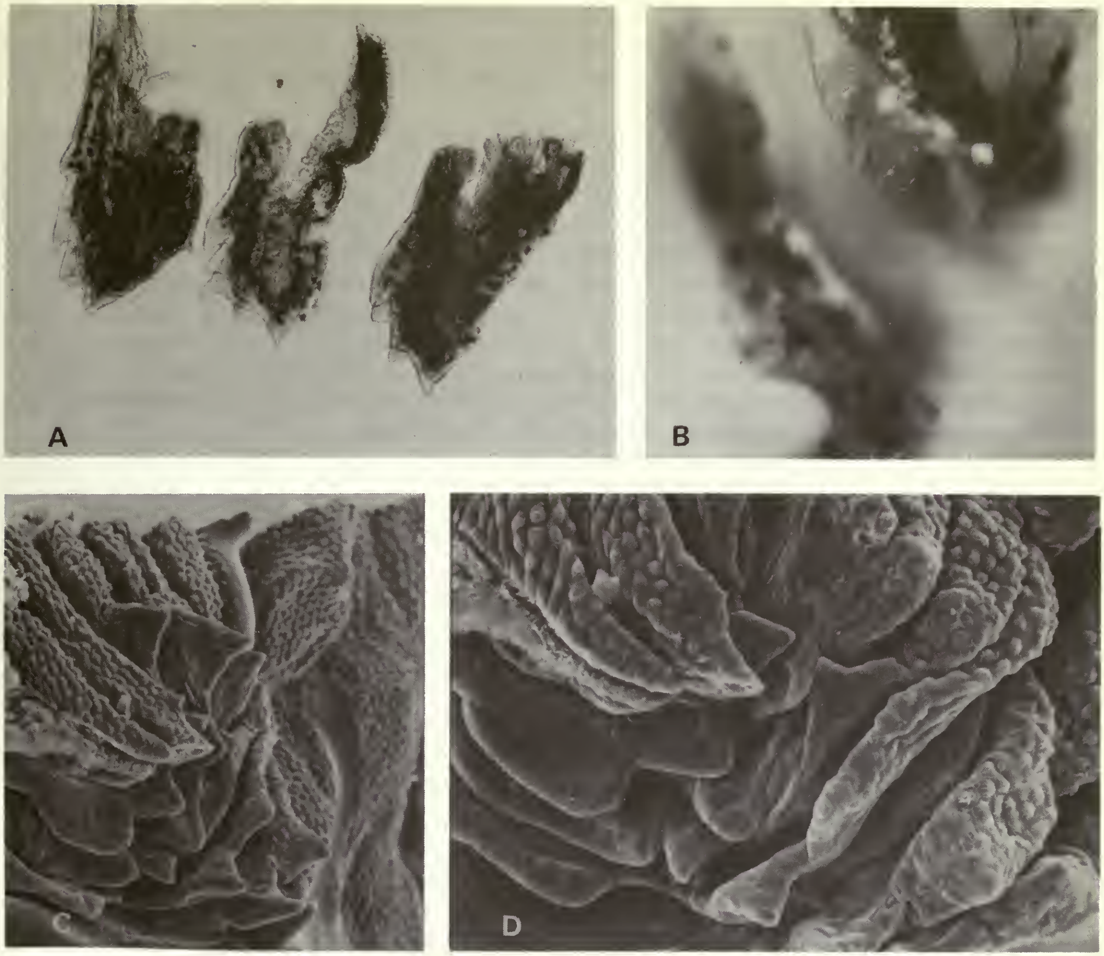

Fig. 2 *Mertensophryne micranotis* sexually mature male: A, three ridges of vent skin dissected and laid flat to illustrate projecting spines on medial surface, × 6; B, sagittal section of the cloacal tube showing spines on lining of the tube and at its aperture, × 10; C-D, portions of median surface of vent skin, × 151 and 250.

& Rose (1929) who attributed a clutch of 7000 eggs to a 37·0 mm SVL *B. rosei* Hewitt. They do however emphasise in the text of their paper the physical impossibility of such a small toad accommodating such a vast number of eggs. In the course of the present study the total number of enlarged heavily pigmented ova was counted in a 30·0 mm SVL *Bufo rosei*; there were 90 and the diameter of the eggs averaged 2·5 mm. The two ovaries contained about 50 very small unpigmented ova as well. A similar clutch size was found in *Bufo tradouwi* Hewitt. *B. rosei* and *B. tradouwi* have recently been referred to a new genus (Grandison, 1980). The internally fertilised *Nectophrynoides malcolmi* Grandison has the smallest clutch of pigmented eggs (11–31 : M18). Of the six species the amplectic position is unknown in all except *N. malcolmi* in which the male has been reported as assuming a belly to belly position with the female while in lumbar amplexus (Grandison, 1978) and *B. rosei* which Power & Rose (1929) described as being axillary.

If, as the Kenyan material of *M. micranotis* suggests, the species' breeding site is restricted to crevices in rotten trees obtaining proof of the mating position will be difficult. An amplectic pair will have to be carefully winkled out without dislodging the male from the female but if care is exercised it should be possible to extract them by flooding the hole. By maintaining the pairs in captivity for a short time and observing them carefully the function of these cloacal structures may be determined and examination of the eggs and reproductive tract may yield information on whether internal fertilisation is accomplished in *M. micranotis.*

The breeding behaviour and mode of fertilising the eggs remain unknown in numerous species of frogs and toads, particularly the small secretive species. Among African bufonids internal fertilisation has been demonstrated solely in five species of *Nectophrynoides* that produce their young by various forms of direct development, ranging from a terrestrial non-feeding tadpole to true viviparity (Grandison, 1978; Wake, 1980). In one of these five species (*N. occidentalis*) transfer of the sperm to the female is achieved by close apposition of the cloacal openings while the mating pair are in lumbar amplexus (Angel & Lamotte, 1948; Lamotte & Xavier, 1972). But none of these five species of *Nectophrynoides* has any apparent modification of the skin surrounding the cloaca that would lock the vents together during sperm transfer. Investigation of their cloacal muscles may however reveal significant differences from the arrangement in externally fertilised species.

Description of tadpole

Length of stage 30 of Gosner (1960) 13·1 mm. The nostrils and the eyes lie in a saucer-like depression which slants steeply forwards and downwards and is partially surrounded by a raised ring of slightly pigmented tissue, the outer rim of which is incomplete posteriorly where it merges with the trunk (Fig. 3B). Eyes situated at the posterolateral corners of the depression, partly obscured in dorsal view by the overhang of the crown. Orbitonasal line clearly visible. Spiracle single, sinistral, situated 65% posteriorly along trunk, its opening vertically oval, visible laterally. Vent median. Fig. 3C.

Oral disk approximately 40% of head width at level of disk. Rostral papillae absent. No gap in mental papillae. Suprarostrodont and infrarostrodont serrated and keratinized. Keratodonts compound. Keratodont formula I/II (Fig. 3A). Tail with dorsal and ventral fin margins parallel except distally where maximum height increases slightly. Tail tip broadly rounded. Tail appreciably lower than trunk. Axis of tail straight, in line with body axis. Tail length: head and trunk length approximately 2 : 1. Trunk height: height of caudal muscle at tail base 2·5 : 1. Head within 'crown' pigmented, trunk more heavily pigmented, tail unpigmented (Fig. 3C).

Comparison with other African bufonid tadpoles

Stephopaedes anotis and *Mertensophryne micranotis* are the only species of Bufonidae known to have a 'crown' and a continuous fringe of mental papillae with no median gap. A mental gap is characteristic of *Bufo* tadpoles (Channing, 1978). The tadpole of *micranotis* differs from that of *S. anotis* in total length, in having an infrarostrodont, in fewer keratodonts with no interrupted supra-angular series, in tail shape and length and in the less pronounced and incomplete development of the 'crown'. The osteological and external morphological differences between adults of these species will be discussed in a forthcoming paper (Grandison in prep.).

Function of the larval 'crown'

The tadpoles of *Stephopaedes anotis* were described by Channing (1978) as having been found in stagnant pools in tree buttresses and were seen to be clinging to slimy bark in a tail-down position. He suggested that the function of the head 'crown' may be to exclude from the eyes and the nostrils the scum accumulating on the water surface. A similar function may be attributed to the convex ring of tissue on the head of the tadpole of *micranotis*. An alternative hypothesis is that the 'crown' may act as a sucker attaching the angled head to the

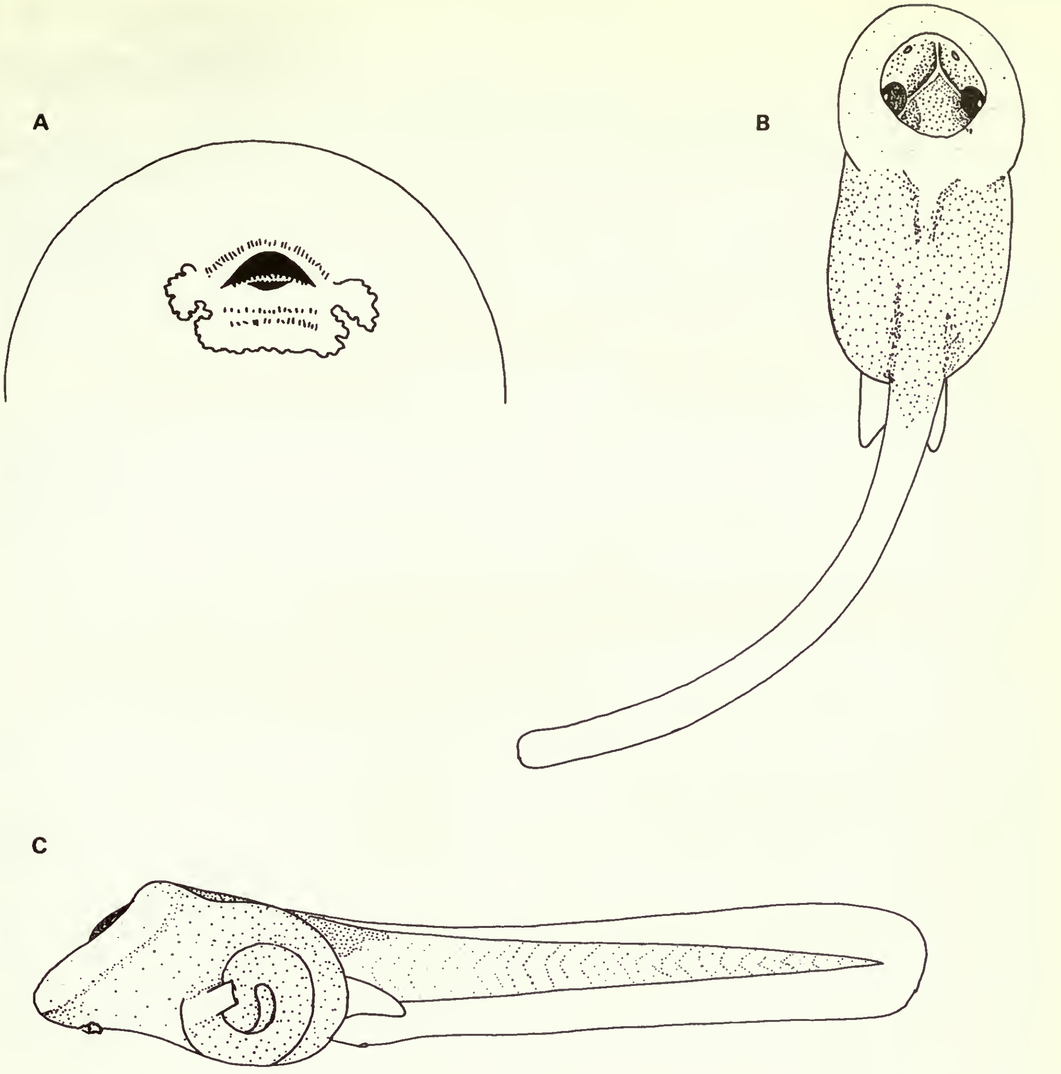

Fig. 3 *Mertensophryne micranotis* stage 30 tadpole: A, mouthparts; B, dorsal view showing the 'crown' surrounding the eyes and nostrils; C, lateral view showing the angular head, ventral mouth and long tail.

lining of the tree hole and allowing the ventrally placed mouth to browse on algae at the base of the hole but this would imply that the tadpole feeds head downwards. Until further field observations on the behaviour of the tadpole and the breeding site become available the function of the crown remains purely speculative.

Many questions relating to the life history and behaviour of this species remain unanswered. Some of them will be answered when amplectic pairs are obtained and fully ripe eggs available. Others, such as does the species select as breeding sites tree holes that are exposed to the elements and fill with water, what are its special requirements on tree hole size and aperture, height of hole from forest floor, type of tree and diameter of its trunk, may necessitate a longer period of field study. It is hoped this note will stimulate an interest in patterns of breeding behaviour in frogs and toads, especially in the small East African toads about which so little is known.

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The author's sincere thanks are also extended to her colleagues Dr H. M. Platt and Mr D. Claugher for assistance with interference contrast microscopy and to Dr J. D. George for his advice.

Materials examined

28 adults and subadults: MCZ 10333 (holotype of *M. micranotis*), MCZ 10334 (paratype of *M. micranotis*), MCZ 25090 (holotype of *M. micranotis rondoensis*), MCZ 25091–94 and MCZ 25098–99 (paratypes of *M. m. rondoensis*), MCZ 32107, MCZ 12455, MCZ 26668, CAS 89737, UMMZ 61367, BM 1947.1.1.51–53, BM 1951.1.8.28, BM 1978.613, A/1150/1–4, A/1265, A/1266, A/1267, A/1268/2, A/1270/1.

28 tadpoles (stages 30–45): A/1150/5–9.

Abbreviations

A	National Museums of Kenya
BM	British Museum (Natural History)
CAS	California Academy of Sciences
MCZ	Museum of Comparative Zoology
UMMZ	Museum of Zoology, University of Michigan

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A new species of *Crocidura* from Nigeria (Mammalia: Insectivora)

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Introduction

During July and August 1978, Dr Andrew Demeter, Zoologist of the Hungarian Natural History Museum at Budapest, collected a large series of owl pellets in the Yankari Game Reserve in Northern Nigeria (see Demeter 1980 for details and a map of the reserve). The owl pellets contained skulls of about 120 Soricidae, which are now under study by the first author. Among them is a series of thirteen skulls of a remarkable new species of shrew, for which we propose the name

Crocidura yankariensis n. sp.

Holotype. Skull of a young adult specimen with occipital region missing, left and right mandibles present, removed from owl pellets collected by Andrew Demeter on 7 August 1978 at Futuk (9°50′N 10°55′E), 16 km E. of the Yankari Game Reserve boundary, Bauchi State, Nigeria; collectors number 32, holotype deposited in the Natural History Museum Budapest, No. HNHM 80.1.1.

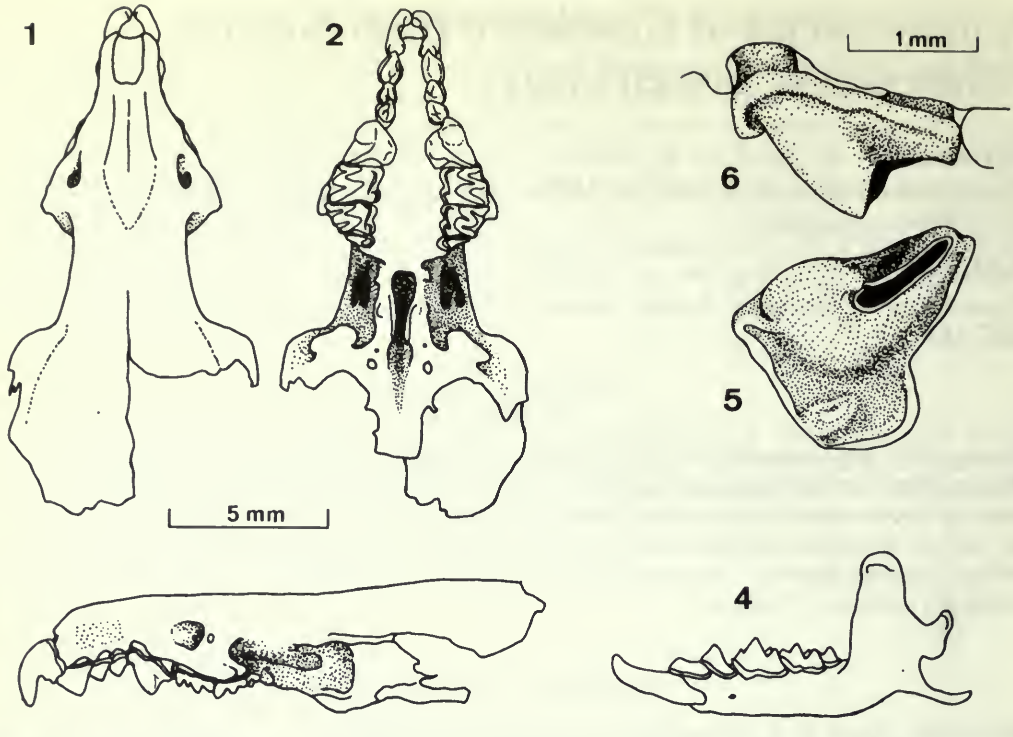
Paratypes. A further nine skulls from Futuk, all data as for the holotype, collectors numbers 30, 31, 33, 36, 44, 47, 51, 54, 55; three skulls from Wikki (9°45′N 10°30′E), a village in the center of the Yankari Game Reserve (see map in Demeter 1980), collected on 25 July and 11 August 1978 by Andrew Demeter; collectors numbers 67, 99, 100. Part of this material will be deposited in the British Museum (Natural History), London, and the Zoologisches Forschungsinstitut and Museum Alexander Koenig, Bonn.

Diagnosis. A small shrew of the genus *Crocidura*, with condyloincisive length 18–19 mm, interorbital constriction fairly narrow, braincase broad, the superior articular facet with a markedly angular crest. The first and second upper incisors and the fourth upper premolar large and heavy, third lower molar minute. Parastyle of the fourth upper premolar absent, but cingulum well developed. First upper molar with a subsidiary cusp. Proto- and metaconid of the first lower molar united.

Description of type series. Thirteen crania, three left and two right mandibles are available. Dental and cranial nomenclature follows Meester (1963), except for the mandibular dentition, for which nomenclature was adapted from Butler & Greenwood (1979).

Skull (Figs 1–3) General construction flat and broad. In the few skulls with intact braincases the breadth of braincase is about 45% of condyloincisive length. Dorsal surface slightly convex, forming a somewhat domed braincase. Superior articular facet of braincase with a well developed angular crest. Interorbital constriction long and narrow. Zygomatic process of the maxillary well developed, its posterior aligned with the middle of the second upper molar, rarely with junction between the first and second upper molars. Mandible without

Bull. Br. Mus. nat. Hist. (Zool.) **39** (5): 305–310 Issued 18 December 1980



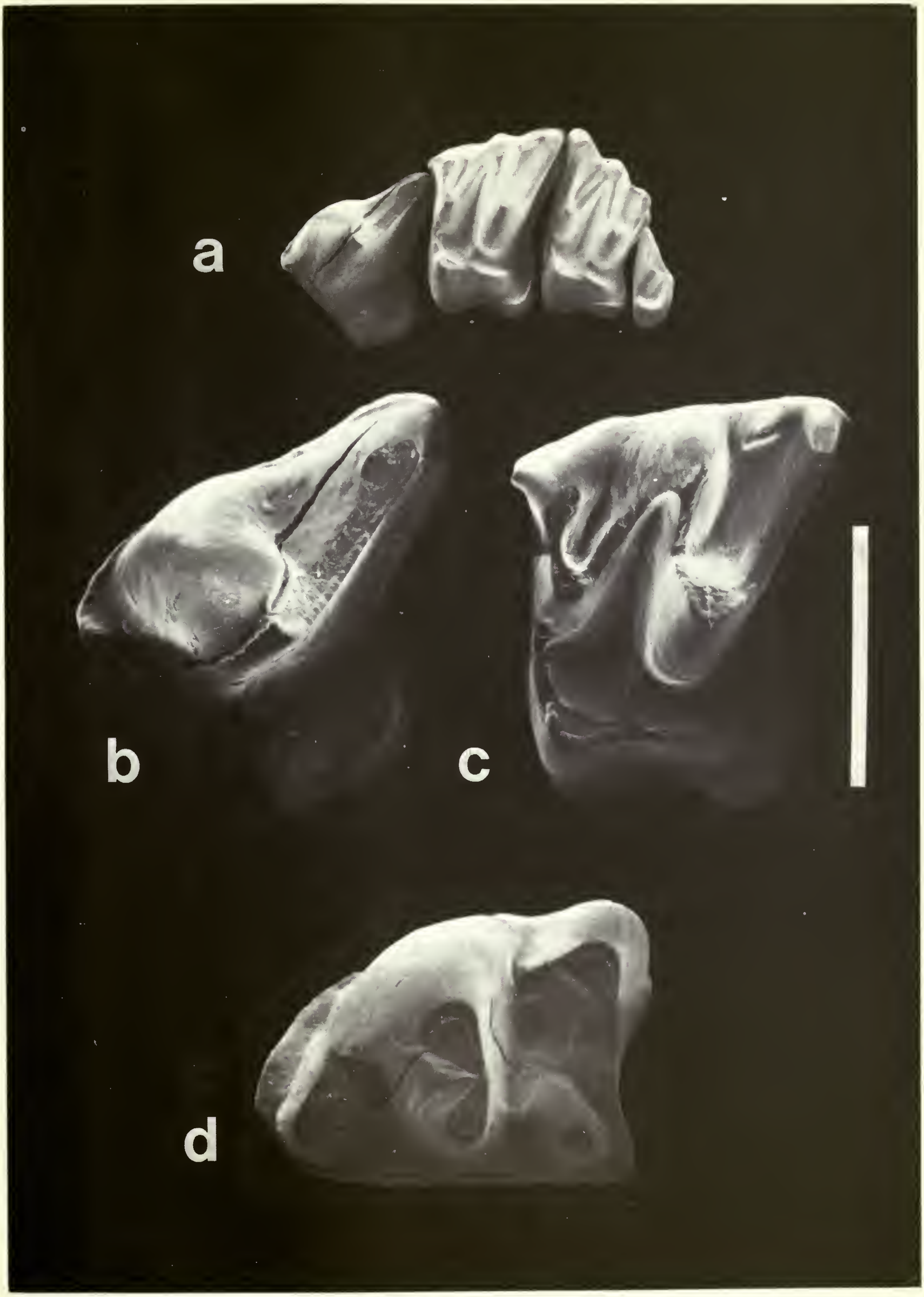
Figs 1–6 Skull and dentition of *Crocidura yankariensis* n. sp., (1–3) paratype, no. 33, (4–6) holotype, no. 32, HNHM 80.1.1.; (1) dorsal view of skull, (2) ventral view of skull, (3) lateral view of skull, (4) lateral view of left mandibular ramus, (5) occlusal view of left P^4, (6) labial view of left P^4.

peculiarities, coronoid process rather high and broad, angular process slender. Mental foramen below the posterior edge of the fourth lower premolar (P$_4$).

Teeth (Figs 2–7). First upper incisor bifid, with a long anterior and a small posterior cusp (Fig. 3); the second incisor also large, twice as large as the following two small unicuspid teeth. The fourth upper premolar (P^4) very robust particularly the large metacone (Figs 5, 6 & 7); the small parastyle is lacking but the cingulum is well developed and forms a small 'cusp' when viewed from the side; the lingual part of P^4 extends far beyond a hypothetical line along the lingual edges of M^1, M^2 and M^3. The first and second upper molars are also characteristic, a subsidiary cusp is present in the valley between the mesostyle, metacone and metastyle on the labial part of M^1, in a few specimens there are traces of such a cusp on M^2; this small but distinct cusp is not visible on the worn teeth of old specimens. Three specimens (31, 33, 54) have a subsidiary cusp on ridge between paracone and mesostyle on labial part of M^1 and also on M^2 in No. 33. There are also indications of a metaconule between the protocone and hypocone of M^1 and M^2, as described by Heim de Balsac & Mein (1971) in a specimen of *Crocidura* sp. (group *dolichura*) from Thebes, Egypt. The third upper molar is small and simple.

Lower incisor smooth, with traces of denticulations only; lower premolars normal; the first lower molar is large and peculiar, since the proto- and metaconid are united and form nearly a joint cusp (Fig. 7d); in the second lower molar the proto- and metaconid are separated by a valley, as usual; the third lower molar is very small, its hypoconid has no fovea.

Fig. 7 *Crocidura yankariensis* n. sp., paratype, no. 55, dentition. (a) Left upper fourth premolar and molar series, (b) P^4 (c) M^1 enlarged, note the subsidiary cusp on M^1, (d) first right lower molar M$_1$. Scanning electron photographs; scales are 1 mm.


a
b
c
d

MEASUREMENTS. See Table 1. Measurements of the type series were taken by Hutterer.

ETYMOLOGY. The specific name has been derived from the type locality, the Yankari Game Reserve.

DISTRIBUTION. *Crocidura yankariensis* is known only from Futuk (9°50′N 10°55′E) and Wikki (9°45′N 10°30′E), Northern Nigeria.

ECOLOGY. As will be demonstrated below, we assume that the new species is a savanna shrew. The Yankari Game Reserve covers a wide range of different vegetation types, ranging from tall swamp forests to open grassland (Geerling, 1980). The larger fauna of the Reserve is typical of West African savanna, and most of the shrews in the Yankari owl pellets are also savanna species, e.g. *Crocidura sericea arethusa* Dollman, 1915, *C. butleri* Thomas, 1911*b*, and others.

Table 1 Cranial and dental measurements (in millimetres) of *Crocidura yankariensis*

	Holotype HNHM 80.1.1.	Type series Mean	Range	n
Length of palate	7·9	7·74	7·2 – 8·0	10
Bimaxillary width	6·0	5·87	5·5 – 6·1	12
Least interorbital width	4·2	4·08	3·8 – 4·4	12
Greatest width	8·2	8·20	8·0 – 8·4	3
Length of upper toothrow	8·2	7·98	7·7 – 8·4	9
Lower toothrow length	7·6	7·63	7·5 – 7·8	3
I^2–I^2 (external)	2·3	2·31	2·2 – 2·5	8
M^2–M^2 (external)	5·5	5·36	5·0 – 5·7	10
Length of mandible	10·1	10·10	10·0 –10·2	3
Height of coronoid process	4·6	4·80	4·6 – 5·0	3
P^4 Length	1·7	1·72	1·7 – 1·8	13
Breadth	1·8	1·76	1·6 – 1·8	13
M^1 Length	1·5	1·51	1·4 – 1·6	12
Breadth	1·6	1·69	1·6 – 1·8	12

Discussion

COMPARISONS. Some characters of *Crocidura yankariensis* appear to be unique among recent African shrews. We have compared our specimens with the holotypes of *C. cinderella* Thomas, 1911*a*, *C. crossei* Thomas, 1895, *C. hildegardae rubecula* Dollman, 1915, *C. ingoldbyi* Heim de Balsac, 1956, *C. jacksoni denti* Dollman, 1915, *C. occidentalis picea* Sanderson, 1940, *C. occidentalis virgata* Sanderson, 1940, *C. pitmani* Barclay, 1932, *C. poensis attila* Dollman, 1915, *C. silacea* Thomas, 1895; with specimens of *C. bicolor* Bocage, 1889, *C. bottegi* Thomas, 1898, *C. dolichura* Peters, 1876, *C. douceti* Heim de Balsac, 1958, *C. floweri* Dollman, 1915, *C. gracilipes* Peters, 1870, *C. lusitania* Dollman, 1915, *C. planiceps* Heller, 1910 and *C. sericea arethusa* Dollman, 1915. For the following forms only descriptions were available to us: *C. bovei* Dobson, 1887, *C. foucauldi* Morales Agacino, 1943, *C. maquassiensis* Roberts, 1946, *C. malani* Lundholm, 1955, and the fossil *C. taungensis* Broom, 1948.

C. yankariensis is most similar in size and overall skull proportions to *C. cinderella*, *C. crossei*, *C. gracilipes* and *C. pitmani* (including *C. maquassiensis* and *C. malani*), while the other species may be discarded. None of the remaining four species has the superior articular facet of the braincase with a markedly angular crest, although some specimens of *C. gracilipes* are fairly angular; *C. crossei* is rounded, *C. cinderella* slightly angular, *C. pitmani* rounded; in *C. maquassiensis* this character has not been described by Roberts (1946), Lundholm (1955) or Meester (1963). *C. pitmani*, *C. maquassiensis* and *C. malani* have a fovea on the hypoconid of M_3, which is not present in *C. yankariensis*.

None of the recent forms that we have compared with *C. yankariensis* has a similarly robust P^4; the absence of the parastyle of P^4 is shared with the fossil *C. taungensis* (see Meester, 1955 for a drawing of the tooth), but the measurements that he gives of the teeth are smaller and the outlines of the teeth in a drawing by Broom (1948) do not correspond to *C. yankariensis*. Meester points out that in all living species of *Crocidura* the anterior cusp is quite well developed. This is correct in general but there are a few exceptions, for instance the holotype of *Crocidura petersii* Dobson, 1890*a* (see Dobson, 1890*b*, Plate 28, Fig. 17). The absence of the anterior cusp is constant in the type series of *C. yankariensis*, so may be regarded as typical for the species.

None of the recent species has a well defined subsidiary cusp on the first upper molar as in *C. yankariensis*. Nor do they have a first lower molar with the proto- and metaconid united.

RELATIONSHIPS. The limited material available to us allows few remarks on the possible relationships of the new species within the genus *Crocidura*. It is difficult to allocate *C. yankariensis* to a definite subgeneric group, because the external features are unknown. Judging from the skull, the general appearance of *C. yankariensis* is that of a savanna shrew, in terms of the flat and broad skull and the fairly narrow interorbital constriction, characters partly shared with *C. sericea* (Sundevall, 1843), *C. butleri* Thomas, 1911*b*, *C. hindei* Thomas, 1904, or *C. lamottei* Heim de Balsac, 1968. However, the ratio of interorbital breadth to maxillary breadth is higher in *C. yankariensis* than these species, which makes it similar to the *gracilipes* group.

The connection between the protocone and hypocone of the upper first and second molars resembles a case described by Heim de Balsac & Mein (1971) in a specimen of the *C. dolichura* species group. A connection between the protocone and hypocone of M^1 and M^2 is also present in the extinct genera *Heterosorex* and *Dinosorex*, members of the subfamily Heterosoricinae, consisting of miocene shrews of Europe and North America (see Engesser, 1975, Plate IV, Figs 1–3). The unique P^4 of *C. yankariensis* is most similar to the P^4 of *Heterosorex delphinensis* Gaillard, 1915 figured by Engesser (1975, Plate IV, Fig. 1) and also to a specimen of *Domnina gradata* Cope, 1873 figured by Repenning (1967, Fig. 3), both species belonging to the Heterosoricinae, a subfamily which is dissimilar to the recent Crocidurinae in several respects. It is also noteworthy that the closeness of the protoconid to the metaconid on M_1 is said by Repenning (1967) to be characteristic of the living crocidurines (subfamily Crocidurinae) and particularly of the extinct limnoecines (subfamily Limnoecinae). To our knowledge, this is generally not the case in *Crocidura*, where both cusps are separated by a valley; the M_1 of *C. yankariensis* with protoconid and metaconid distinctly close together is an exception among *Crocidura* and possibly an ancestral character, although it is difficult to evaluate characters at the present level of knowledge. New material and a better understanding of the whole genus is required to fix the exact position of *C. yankariensis*. At present it is wiser to avoid extended speculation.

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